UNIVERSITÉ DU QUÉBEC À MONTRÉAL

L'ÉCOLOGIE FONCTIONNELLE : UNE APPROCHE POUR MIEUX COMPRENDRE LE RÔLE DU PLANCTON DANS LES LACS

THÈSE

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RÉSUMÉ

Même si plusieurs études ont montré qu'il existe une relation entre la diversité d'une communauté et sa production de biomasse, l'applicabilité de cette hypothèse à divers écosystèmes naturels est encore débattue. Cette question est spécialement importante pour les écosystèmes aquatiques, puisque la littérature tend à démontrer que la relation positive entre la diversité et la production de biomasse y est rarement observée. Dans les lacs, le zooplancton représente un niveau intégrateur d'une grande importance pour le transfert d'énergie à l'intérieur du réseau trophique.

L'objectif principal de la présente thèse est donc de comprendre l'importance de la structure fonctionnelle des communautés zooplanctoniques comme facteur régulant la productivité zooplanctonique dans les lacs tempérés nordiques. Cependant, afin d'évaluer l'effet de la structure des communautés, en termes de diversité et de composition, sur la productivité zooplanctonique dans les lacs, il est important de tout premièrement considérer l'effet de l'environnement sur la productivité ainsi que sur la structure des communautés. À l'intérieur de chacun des chapitres de la thèse, nous avons utilisé une approche basée sur les traits fonctionnels, pour analyser les liens entre la structure des communautés, leur métabolisme et leur environnement. Plus précisément, afin d'améliorer notre compréhension des liens qui existent entre la structure des communautés planctoniques, leur environnement et la productivité zooplanctonique, nous les avons caractérisés conjointement à l'intérieur de plus de 100 lacs tempérés nordiques. Par la suite, nous avons évalué l'applicabilité de nos conclusions à grande échelle en utilisant la même approche, mais dans le contexte d'une perturbation anthropique importante. Spécifiquement, nos objectifs visent : (1) à comprendre l'effet des interactions trophique sur la distribution du zooplancton et phytoplancton à l'échelle du limnopaysage, en comparaison de l'effet de la qualité de l'eau et de l'habitat (2) à identifier les facteurs environnementaux affectant la productivité zooplanctonique au niveau de la communauté et (3) à comprendre l'importance relative de la structure des communautés et de l'environnement sur la productivité zooplanctonique. Finalement, nous avons testé spécifiquement quelle était la réponse de la communauté planctonique à un changement important dans la qualité de l'eau résultant d'une activité minière. De plus, nous avons comparé cette réponse à ce qui fut observé dans notre étude à grande échelle.

Pris collectivement, nos résultats ne montrent un couplage trophique entre la composition du phytoplancton et du zooplancton, autant à l'échelle du paysage que dans le cas d'une importante pression anthropique. Cette absence de couplage au niveau du limnopaysage résulte des réponses distinctes du phytoplancton à la qualité de l'eau et du zooplancton à la morphométrie du lac. Une des conséquences importantes l'absence de couplage sur les lacs en aval de la mine est qu'en 20 ans l'effet de la mine sur les communautés planctoniques s'est limité à la base du réseau trophique (au phytoplancton). Au niveau de la productivité zooplanctonique, en plus de l'effet de la température, de la biomasse de phytoplancton et de la taille moyenne des individus, tel que précédemment observé au niveau de la population, nous avons identifié la taille du lac et la couverture des milieux humides dans le bassin versant comme variables émergentes au niveau de la communauté. Ces variables émergentes suggèrent une certaine importance de la structure des communautés sur la productivité planctonique. Nous avons pu le confirmer en testant directement l'effet de la diversité et de la composition zooplanctonique sur la productivité zooplanctonique. Nous avons observé que l'importance relative de la structure des communautés et de l'environnement comme facteurs qui influencent la production zooplanctonique étaient comparables. Cependant, nous avons observé que l'effet de la structure des communautés sur la productivité zooplanctonique ne se situe pas au niveau de la diversité fonctionnelle, mais plutôt au niveau de la composition fonctionnelle. Plus précisément, nous avons observé que la productivité zooplanctonique est plus élevée dans les communautés à l'intérieur desquelles les stratégies alimentaires *daphnia*-filtration et *chydorus*-filtration sont dominantes. De plus, nous avons observé une forte relation négative entre la productivité planctonique et l'équitabilité fonctionnelle, qui s'explique par le fait que la stratégie alimentaire change au cours de la succession saisonnière. En conclusion, nous avons démontré qu'il existait un effet important de la structure des communautés sur la productivité planctonique. À l'échelle du limnopaysage la composition du zooplancton répond principalement à la morphométrie du lac, ce qui explique qu'il n'existe aucun couplage significatif avec la composition du phytoplancton, ainsi que l'absence de réponse de la composition du zooplancton dans les lacs miniers.

INTRODUCTION

0.1 L'importance du plancton dans la chaine trophique aquatique

Étant à la base de la mobilisation et du transfert de la majorité de l'énergie et de la matière disponible dans les écosystèmes aquatiques boréaux (Kankaala *et al.*, 2013), les communautés zooplanctonique et phytoplanctonique (ou communauté planctonique) jouent un rôle primordial à l'intérieur du réseau trophique aquatique. En comparaison aux herbivores terrestres, les herbivores aquatiques (le zooplancton) consomment une beaucoup plus grande proportion de la production primaire (en moyenne 80% versus 30% pour les écosystèmes terrestres, Cyr et Pace, 1993). Considérant l'importance de ce lien trophique, toute variation du phytoplancton ou du zooplancton aura un impact important sur le transfert d'énergie à l'intérieur du réseau trophique d'un lac.

L'interface plante-animal du compartiment planctonique des écosystèmes aquatiques représente donc un lien trophique important au niveau du transfert de biomasse dans l'écosystème aquatique (voir Sterner, 1989). Plusieurs interprétations ont été évoquées pour expliquer la force de ce lien trophique. Premièrement, les algues représentent une source nutritionnelle de qualité pour le zooplancton (Elser *et al.*, 2001) et possèdent relativement peu de défenses physiques et chimiques (Likens, 2009). Elles représentent donc une ressource de qualité qui est facilement accessible. Deux concrétisations importantes de cette interaction entre le phytoplancton et le zooplancton crustacé dans les lacs sont : la phase d'eau claire (Lampert *et al.*, 1986; Talling, 2003) et la succession saisonnière (tel que décrite dans le modèle PEG, Sommer *et al.*, 1986). Cependant, même s'il est re-

connu que le phytoplancton, en tant que ressource, a une grande importance pour le zooplancton crustacé; il en est de même pour la prédation par les poissons et autres invertébrés (Likens, 2009). L'importance relative de ces deux processus (Brett et Goldman, 1997) sur les communautés planctoniques est encore débattue et peu d'études ont approché la question à l'échelle du paysage des lacs. Ces deux processus ont un effet structurant sur la communauté zooplanctonique, tant pour la biomasse (par exemple les cascades trophiques, Carpenter *et al.*, 1985) que sur la composition en espèces (McQueen *et al.*, 1989; Ghadouani *et al.*, 2003). Bien que le lien trophique existant entre la biomasse des deux communautés soit mieux compris (voir Sommer *et al.*, 2012), peu d'études à grande échelle ont directement testé l'effet de cette interaction trophique sur la distribution du phytoplancton et du zooplancton.

0.2 Les facteurs contrôlant la productivité zooplanctonique

Sur le plan écosystémique, la compréhension des facteurs qui influencent la productivité d'un lac (l'efficacité du transfert d'énergie et de matière dans le réseau trophique), exige de bien comprendre les facteurs régulant la production planctonique. Bien qu'il est généralement reconnu que la lumière et la concentration de nutriments influencent grandement la production phytoplanctonique (Kalff, 2002), pour le zooplancton les facteurs régulant sa production de biomasse ne sont toujours pas bien connus. De plus, pour les lacs boréaux, la pénétration de la lumière est aussi identifiée comme facteur influençant grandement la production de biomasse des poissons (Karlsson *et al.*, 2009; Benoit *et al.*, 2016). Il y a un manque important de connaissance au niveau trophique du zooplancton, un niveau trophique important, puisqu'il intègre la biomasse produite par les mobilisateurs d'énergie dans les lacs. Ce manque d'information s'explique principalement par les défis méthodologiques que représentent les études à grande échelle de la production zooplanctonique. Au niveau d'organisation des populations, il est bien

connu que la température, la taille des organismes et la qualité de la nourriture disponible sont les principaux facteurs contrôlant le taux de production de biomasse zooplanctonique (Brown *et al.*, 2004; Lin *et al.*, 2013; Downing et Rigler, 1984). Cependant, nous ne comprenons toujours pas si les mêmes facteurs biotiques et abiotiques contrôlent la productivité zooplanctonique de la communauté ou si d'autres variables sont émergentes à ce niveau.

0.3 L'influence de la structure des communautés planctoniques sur la productivité

Une question importante en écologie est de savoir si une communauté peut être considérée comme une boite noire répondant seulement aux variations de son environnement, telle qu'elle le fut traditionnellement. Il y est cependant de plus en plus clair que de concevoir les communautés comme des boites noires est trop réducteur et que la structure des communautés influence aussi leur métabolisme (voir Cardinale *et al.*, 2012; Hooper *et al.*, 2005). Pour l'écologie des communautés, cette transition constitue un important changement de paradigme (Naeem, 2002). L'idée que la distribution des espèces et leur abondance soit simplement une conséquence de la variation des conditions abiotiques, à plus grande échelle, et des interactions biotiques, à plus petite échelle, est de plus en plus remise en question (Naeem, 2002). L'effet de la structure des communautés, et principalement de la biodiversité sur les processus écosystémiques (BEF, voir Cardinale *et al.*, 2012), est de plus en plus reconnu. De multiples études, théoriques, expérimentales et observationnelles, ont spécifiquement démontré qu'il existait, dans certaines situations, un lien causal entre la diversité des communautés et leur efficacité à produire de la biomasse (voir Balvanera *et al.*, 2006). Même si l'accent initial a principalement été mis sur l'effet de la richesse spécifique, il fut démontré que la composition spécifique peut aussi affecter le métabolisme des communautés et leurs fonctions dans les écosystèmes (Downing et Leibold, 2002). En général, deux mécanismes sont in-

voqués pour expliquer l'effet de la diversité et de la composition sur la productivité d'une communauté (Cardinale *et al.*, 2009). Premièrement, pour expliquer pourquoi une communauté plus diverse serait plus productive, le mécanisme le plus fréquemment utilisé est celui de la complémentarité. Celle-ci s'explique par un plus important partitionnement des niches écologiques ainsi qu'une augmentation de la facilitation entre les espèces lorsque la diversité est plus grande (voir Tilman, 1999). Deuxièmement, le mécanisme de la sélection est basé sur l'idée que certaines espèces sont fondamentalement plus productives que d'autres. Conséquemment, une communauté sera plus productive en moyenne lorsque ces espèces seront plus abondantes (Aarssen, 1997; Huston, 1997). Bien que cette deuxième hypothèse ne soit pas directement liée à la diversité, une communauté plus diverse a plus de chance d'inclure des espèces productives.

Après près d'une vingtaine d'années de recherches sur le sujet, il fut conclu qu'en général les écosystèmes avec une plus grande diversité en espèces sont plus productifs (Cardinale *et al.*, 2012). Cependant, en considérant les études réalisées dans les milieux aquatiques (Figure 0.1), il est loin d'être clair que cette conclusion y soit applicable, puisqu'elles n'ont eu en majorité rapporté aucune relation significative entre la diversité et la production de biomasse dans les écosystèmes aquatiques. Les quelques-unes les études qui ont détecté une relation entre la diversité et la production de biomasse,ont a trouvé une relation négative (voir Figure 0.1). Cette différence entre les communautés aquatiques et terrestres peut s'expliquer par les multiples différences qui existent entre les écosystèmes aquatiques et terrestres. Par exemple, l'eau est un médium qui favorise le transfert rapide d'énergie et de matière (Warwick et Clarke, 2001) . De plus, à l'intérieur d'un seul lac, la diversité d'habitat est importante (Giller *et al.*, 2004) et l'environnement change constamment. Par conséquent, les communautés à la base des réseaux trophiques aquatiques et terrestres ont un cycle de vie complètement différent. Il est donc pos-

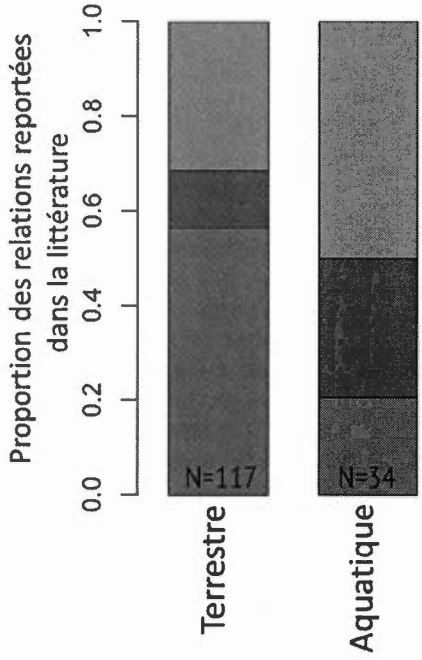

Figure 0.1 Sommaire des relations rapportées dans la littérature entre la biomasse ou le taux de production de biomasse et la diversité (positives en vert, négatives en rouges, absence de relation en gris) dans les écosystèmes terrestres et aquatiques. Les données proviennent de Balvanera et al. 2006 et Rohr et al. 2016.

sible que la relation entre la diversité et la production de biomasse soit différente entre les deux types d'écosystèmes.

0.4 L'écologie fonctionnelle comme outil pour comprendre les liens entre la structure des communautés et leur métabolisme

En parallèle à l'important changement de paradigme concernant le rôle écosystémique des communautés, les écologistes remettent de plus en plus en question la façon de caractériser ces dernières. En effet, la structure d'une communauté peut être caractérisée de multiples façons. Traditionnellement, la mesure la plus souvent utilisée fut la diversité taxonomique et plus particulièrement la richesse spécifique,

qui est facile à interpréter et à calculer. D'une façon complémentaire, la composition taxonomique permet de caractériser un aspect différent de la structure d'une communauté, étant basée sur l'identité des espèces présentes.

Afin de comprendre comment une communauté interagit avec son environnement, l'utilisation des méthodes basées sur la taxonomie n'est pas optimale, car elle ne tient pas en compte la façon dont les organismes interagissent avec leur environnement. Il est reconnu que les organismes interagissent avec leur environnement (répondent et affectent) par l'interface de leurs traits fonctionnels (Díaz et Cabido, 2001; Hooper *et al.*, 2005; Violle *et al.*, 2007; Cadotte *et al.*, 2011). Une approche par traits fonctionnels permet donc de caractériser une communauté en utilisant des traits qui sont directement liés à la façon dont elle interagit avec son environnement et conséquemment de mieux comprendre cette interaction d'une façon mécanistique. Plus précisément, en caractérisant la distribution de la fonction des organismes dans une communauté, il est possible d'estimer la complémentarité ainsi que la redondance fonctionnelle entre les espèces. Ceci est particulièrement important pour des communautés où la redondance fonctionnelle entre les espèces est importante, comme c'est le cas des communautés planctoniques, car une approche taxonomique sous-estimerait la redondance fonctionnelle entre les espèces. Les approches basées sur les traits fonctionnels sont donc très prometteuses. En ce sens, il fut démontré que la relation entre la diversité fonctionnelle et les processus écosystémiques (production, décomposition, etc.) est plus forte que celle entre la diversité taxonomique et les processus écosystémiques (Heemsbergen *et al.*, 2004; Mokany *et al.*, 2008).

L'utilisation d'une approche utilisant la diversité et la composition fonctionnelle permet donc de mieux comprendre les liens entre les communautés et comment elles répondent aux variations environnementales à l'échelle du paysage des lacs. De plus, puisque les interactions trophiques sont importantes à l'intérieur des lacs,

cette approche permet de mieux comprendre les liens qui existent entre les différents niveaux trophiques. De la même façon, l'utilisation d'une approche fonctionnelle permet d'identifier quels seront les impacts d'un changement dans la structure des communautés planctoniques sur leur métabolisme ainsi que sur les autres niveaux trophiques.

Il existe de multiples façons de caractériser la structure fonctionnelle d'une communauté (voir Ricotta, 2005; Villéger *et al.*, 2008). Une des méthodes les plus utilisées pour sa relative simplicité est basée sur la construction d'un espace fonctionnel à l'intérieur duquel il est possible de mesurer la distance fonctionnelle entre les espèces. Plus précisément, cette technique consiste à construire un espace fonctionnel à l'intérieur duquel chaque trait est représenté par un axe dans cet espace. Par la suite, pour chaque site, toutes les espèces présentes dans la communauté sont positionnées à l'intérieur de cet espace en utilisant la valeur des traits fonctionnels associée à chaque espèce (Villéger *et al.*, 2008; Laliberté et Legendre, 2010). Il est possible d'utiliser différents indices (richesse, équitabilité, diversité) pour caractériser l'espace fonctionnel de chaque site et de les comparer entre eux. De plus, afin de suivre aussi les changements de la composition fonctionnelle, il est possible d'utiliser la position de chaque espèce à l'intérieur de l'espace fonctionnel.

0.5 L'utilisation d'une approche fonctionnelle pour comprendre la réponse à une perturbation anthropique.

Dans le cadre d'une pression anthropique, l'utilisation d'une approche fonctionnelle peut faciliter la compréhension de la réponse d'une communauté à cette perturbation. Plus précisément, pour comprendre l'impact d'un stresseur sur la structure d'une communauté, il s'agit de quantifier la magnitude et le signe de la réponse des différents traits fonctionnels, ou encore des différents indices de diversité fonctionnelle, à ce stresseur. Une meilleure compréhension des mécanismes

expliquant la réponse d'une communauté permet aussi de mieux anticiper la réponse de cette communauté dans le temps et de prévoir l'impact potentiel sur le reste du réseau trophique. Finalement, pour une communauté qui a un temps de génération court, comme les communautés planctoniques, il est possible d'utiliser cette réponse fonctionnelle comme un indicateur précoce de l'impact d'une stresseur sur un écosystème aquatique (Whitton *et al.*, 1991; Carvalho *et al.*, 2013; Khalifa *et al.*, 2015) .

0.6 Objectif de la thèse

Autant d'un point de vue théorique qu'appliqué, il est crucial de développer une meilleure compréhension des mécanismes qui lient la structure des communautés, leur environnement biotique et abiotique ainsi que leur métabolisme au sein de l'écosystème aquatique. Malgré une bonne compréhension générale de la réponse des différentes espèces aux variations de leur environnement, notre compréhension de la façon dont les interactions trophiques influencent la distribution des organismes (Chapitre I) demeure limitée et ce bien même qu'elles soient d'une grande importance dans les lacs. Au niveau de métabolisme, notre compréhension de l'effet de ces variations de la structure des communautés aquatiques à l'échelle du paysage des lacs sur l'efficacité de ces dernières à produire de la biomasse, est aussi très limitée (Chapitre III). Afin de bien comprendre les liens qui existent entre la structure des communautés planctoniques dans les lacs et la production de biomasse, il est primordial de bien comprendre au préalable comment le taux de production de biomasse répond aux variations des facteurs environnementaux dans les lacs (Chapitre II). Sur le plan appliqué, puisque les écosystèmes aquatiques subissent des pressions anthropiques grandissantes, mieux comprendre les relations entre les communautés, leur environnement et leur métabolisme à l'intérieur du réseau trophique d'un lac est une étape cruciale qui permettra de mieux comprendre quels seront les impacts de ces pressions anthropiques grandissantes

sur l'écosystème et comment un changement à l'intérieur d'une de ces composantes influencera le reste de l'écosystème.

L'objectif principal de la présente thèse consiste à mieux comprendre comment les interactions biotiques et l'environnement influencent la structure des communautés planctoniques dans les lacs tempérés nordiques et comment l'effet des changements dans la structure des communautés planctoniques affectent la production de biomasse à l'échelle du paysage (Figure 0.2). Nous avons utilisé une démarche séquentielle nous permettant de bien comprendre au préalable les relations entre chacune des composantes (l'environnement, la structure des communautés et la productivité). Pour ce faire, en premier lieu, nous avons emprunté une perspective biogéographique pour analyser un jeu de données que nous avons récolté simultanément à l'intérieur de lacs couvrant un important gradient environnemental et morphologique à l'échelle régionale. Par la suite, nous avons employé une perspective spatiotemporelle pour comprendre l'effet d'une importante pression anthropique (activité minière) sur les interactions trophiques au sein de la communauté planctonique. Pour chacune de ces étapes de notre démarche, nous avons utilisé une approche par traits fonctionnels afin de comprendre les mécanismes expliquant les liens entre les caractéristiques d'un écosystème, les communautés planctoniques qui y résident et la production de biomasse. L'approche par traits fonctionnels permet aussi d'extraire des patrons généralisables et prédictibles. Pour atteindre ces objectifs, la présente thèse est sous-divisée en quatre chapitres sous forme d'article répondant aux questions suivantes :

Chapitre 1 : Quelle est l'influence des interactions trophiques et de l'environnement sur la distribution des espèces ainsi que des types fonctionnels de phytoplancton et de zooplancton dans les lacs tempérés nordique à l'échelle du paysage des lacs ?

Chapitre 2 : Quels facteurs environnementaux influencent la productivité zoo-

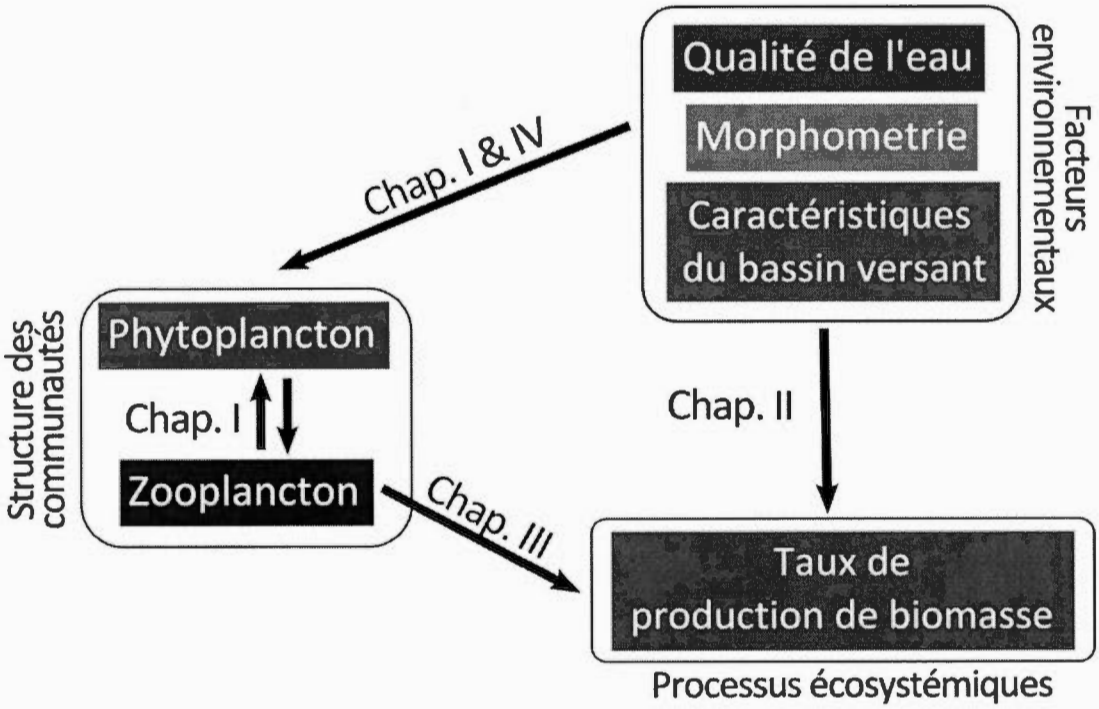

Figure 0.2 La relation entre la structure des communautés planctoniques, les facteurs environnementaux et le taux de production de biomasse zooplanctonique telle que développé dans la thèse.

planctonique de la communauté dans les lacs tempérés nordiques ?

Chapitre 3 : Quelle est l'importance de la structure des communautés zooplanctoniques sur leur efficacité à produire de la biomasse ?

Chapitre 4 : Quelle est la réponse spatiotemporelle des communautés planctoniques à une activité minière intensive ?

0.7 Approche générale et échantillonnage

0.7.1 Perspective biogéographique

Les trois premiers chapitres de la thèse portent sur des données récoltées lors d'un échantillonnage à grande échelle dans les lacs tempérés nordiques de la province du Québec au Canada (voir Figure 1.1). Trois régions de Québec couvrant un important gradient autant au niveau environnemental que géologique (voir Figure 1.1) ont été ciblées lors de l'échantillonnage soit : l'Abitibi, le Saguenay-Lac-Saint-Jean et la région de Schefferville (qui fait partie de la Côte-Nord). À l'intérieur de ces trois régions, la sélection des lacs fut semi-aléatoire puisque les lacs devaient être accessibles par la route, pour un échantillonnage en chaloupe, ou suffisamment grands pour permettre l'amerrissage d'un hydravion pour l'échantillonnage.

Les données biotiques (communautés planctoniques et production zooplanctonique) et abiotiques (variables physicochimiques) ont été récoltées simultanément, majoritairement en été, au point estimé le plus profond du lac. La communauté zooplanctonique a été échantillonnée dans la totalité des lacs et la communauté phytoplanctonique a été échantillonnée pour un sous-ensemble aléatoire de lacs provenant des trois régions. Pour quantifier le métabolisme des lacs, nous avons aussi mesuré la production planctonique à l'intérieur de chacun des lacs en utilisant une méthode enzymatique novatrice. L'enzyme utilisée, la chitobiase, est produite lors de la mue des zooplanctons crustacés et peut être utilisée afin d'intégrer le taux de production de biomasse par la communauté zooplanctonique dans un lac à court terme. Finalement, les caractéristiques du lac (morphométrie) et du bassin versant (utilisation du territoire) ont été estimées à l'aide d'un logiciel SIG (Quantum GIS).

0.7.2 Perspective spatiotemporelle

Pour le dernier chapitre, nous avons utilisé les données spatiotemporelles de la structure des communautés planctoniques et de la physicochimie des lacs en aval d'une mine de diamant, au nord de Yellowknife dans les Territoire du Nord-Ouest au Canada. Pour ce chapitre, les données ont été récoltées annuellement (1997-2014) dans cinq lacs en aval de la mine de diamant Ekati, ainsi que dans deux lacs de références situés dans des bassins versants différents. Afin de comprendre la réponse fonctionnelle des communautés planctoniques en aval de la mine dans le temps et dans l'espace, nous avons utilisé une approche spatiotemporelle. Dans chacun des lacs, les communautés zooplanctonique (zooplanctons crustacés et rotifères) et phytoplanctonique furent échantillonnées à chaque année à la même période, et en même temps que les différentes variables physicochimiques. Tel qu'utilisé précédemment, nous avons caractérisé la morphométrie des lacs en aval de la mine afin de contrôler son effet sur la réponse des communautés en utilisant un SIG.

0.7.3 L'Écologie fonctionnelle en écologie des communautés

L'écologie des communautés est la science qui étudie les variations spatiales et temporelles des communautés biotiques et les processus qui les expliquent (Vellend, 2010). Puisqu'une communauté est un niveau d'organisation biologique complexe, il existe de multiples façons de la caractériser. En général, la diversité et la composition spécifique sont les deux mesures les plus fréquemment utilisées pour en caractériser la structure. Cependant, il est maintenant reconnu que de comprendre le rôle fonctionel d'une communauté à l'intérieur d'un écosystème, les méthodes basées sur les traits fonctionnels des espèces sont supérieures à une approche taxonomique (Díaz et Cabido, 2001; Cadotte *et al.*, 2011; Mouchet *et al.*, 2010). Conséquemment, un nombre grandissant d'études utilisent maintenant une

approche fonctionnelle. L'utilisation de traits fonctionnels, qui sont à l'interface entre les autres composantes de l'écosystème et les communautés biotiques, permet d'identifier et de comprendre la réponse fonctionnelle d'une communauté aux variations dans son environnement. De plus, l'utilisation de cette approche permet d'identifier comment un changement fonctionnel au niveau de la communauté affecte les autres composantes de l'écosystème. Finalement, étudier les traits fonctionnels plutôt que les espèces permet aussi d'identifier des patrons qui seront par la suite généralisables et prévisible (McGill *et al.*, 2006).

Pour l'étude de la diversité, une approche fonctionnelle permet de contrôler pour le chevauchement fonctionnel entre les différentes espèces, et conséquemment d'estimer la diversité des stratégies déployées au sein d'une communauté. En ce qui a trait à la composition, les avantages d'une approche fonctionnelle sont également importants, car cette approche permet de cerner spécifiquement comment certains traits fonctionnels d'intérêt répondent aux différents gradients environnementaux. Ceci est beaucoup plus pertinent et généralisable d'un point de vue écosystémique que d'identifier les espèces répondant à un changement environnemental.

Autant au niveau de la diversité que de la composition fonctionnelle, la sélection des traits fonctionnels utilisés est une décision importante qui peut influencer le résultat de cette méthode (Leps *et al.*, 2006). En général, il existe deux catégories de traits fonctionnels : les traits effets desquelles les organismes affectent leur environnement et les traits réponses, desquelles les organismes répondent à leur environnement (Hooper *et al.*, 2002; Lavorel et Garnier, 2002). Il n'est cependant pas nécessairement évident de diviser les traits dans ces deux catégories puisque plusieurs traits, telle la taille, vont moduler la réponse et l'effet d'un organisme sur son environnement. Au-delà de la sélection de traits effets ou réponses, la sélection de traits fonctionnels en lien avec la question de recherche est primordiale afin d'être en mesure de détecter la réponse anticipée (Leps *et al.*, 2006). Dans la

présente thèse, nous avons sélectionné des traits fonctionnels reflétant les interactions entre les communautés biotiques et leur environnement ainsi qu'entre les différents niveaux trophiques. Plus spécifiquement, nous avons utilisé des traits se rapportant à l'acquisition de ressources, à la prédation, ainsi qu'à la taille, qui est un trait intégrant divers processus écologiques(Litchman *et al.*, 2013; Hébert *et al.*, 2016). Les traits fonctionnels des zooplanctons et phytoplanctons ont été obtenus à partir de la littérature scientifique (Barnett *et al.*, 2007; Longhi et Beisner, 2010, voir les différents chapitres).

Comme pour le niveau taxonomique, il existe de multiples façons d'estimer la diversité et ses deux composantes : la richesse et l'équitabilité fonctionnelle (Mason *et al.*, 2005). Dans cette thèse, nous avons utilisé une approche basée sur un espace multidimensionnel à l'intérieur duquel chaque axe représente un trait. Cette approche par espace multidimensionnel simplifie grandement l'interprétation et la compréhension de la façon dont les différents indices de diversité fonctionnelle sont calculés (voir Villéger *et al.*, 2008; Laliberté et Legendre, 2010). Les différentes caractéristiques de l'espace fonctionnel de chaque communauté seront par la suite utilisées afin de caractériser la diversité fonctionnelle des différentes communautés. Pour ce faire, nous avons sélectionné des indices de diversité qui permettent d'estimer : (i) la taille de la niche fonctionnelle occupée par une communauté (richesse), ainsi que (ii) la façon dont cette niche est occupée (uniformité, dispersion, etc.). Nous avons utilisé deux indices de Villéger (Villéger *et al.*, 2008), l'équitabilité et la richesse fonctionnelle, ainsi que la dispersion fonctionnelle de Laliberté et Legendre (Laliberté et Legendre, 2010).

0.7.4 Approche statistique

La thèse est basée sur différentes analyses statistiques multivariées qui ont été utilisées afin de mieux quantifier les liens existant entre l'environnement, la struc-

ture et le métabolisme des communautés. Pour les deux chapitres (II et III) ayant comme variable réponse centrale le taux de production de biomasse zooplanctonique, nous avons utilisé l'analyse en équation structurelle (Bollen, 1989; Shipley, 2002). Cette méthode permet d'identifier les variables biotiques et abiotiques qui contrôlent la productivité, de quantifier leur importance relative et de comprendre les liens entre les différentes variables explicatives. Pour les chapitres (I et IV) où la variable réponse d'intérêt est la structure taxonomique et fonctionnelle des communautés planctoniques, nous avons utilisé différentes approches multivariées, généralement basées sur l'analyse de redondance (RDA, voir Legendre et Legendre, 1998), permettant l'utilisation d'une variable réponse multivariée.

0.7.5 Taux de production zooplanctonique

La mesure du taux de production de biomasse zooplanctonique est centrale à la présente thèse. Nous devions utiliser une méthode nous permettant d'estimer le taux de production de biomasse dans un grand nombre de lacs, ce qui n'avait jamais été fait. Cependant, les techniques traditionnellement utilisées pour mesurer la productivité zooplanctonique dans les lacs demandent un échantillonnage intensif (voir Dolbeth et Cusson, 2012), ce qui les rend inapplicables à petite échelle, lorsqu'un grand nombre de lacs doit être échantillonné. Nous avons donc utilisé une technique enzymatique novatrice basée sur la chitobiase (voir Sastri et Roff, 2000; Sastri *et al.*, 2013, pour plus de détails) pour mesurer le taux de production de biomasse par les zooplanctons crustacés. Cette méthode, basée sur un seul échantillon d'eau, permet d'estimer le taux de production de biomasse des zooplanctons crustacés *in situ* et intègre la production de biomasse sur un court laps de temps.

CHAPITRE I

THE TAXONOMIC AND FUNCTIONAL BIOGEOGRAPHIES OF PHYTOPLANKTON AND ZOOPLANKTON COMMUNITIES ACROSS BOREAL LAKES

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N.B. References cited in this chapter are presented at the end of the thesis

1.1 Abstract

Strong trophic interactions link primary producers (phytoplankton) and consumers (zooplankton) in lakes.However, the influence of such interactions on the biogeographic distribution of taxa or functional traits has never been explicitly tested. To better understand the ecological interactions of these two major trophic groups, we related the distributions of their taxa and functional traits across 104 boreal lakes to a common suite of environmental and spatial factors. We directly tested the degree of coupling in their taxonomic and functional distributions. Phytoplankton functional composition responded mainly to properties related to water quality, while zooplankton composition responded more strongly to lake morphometry. Overall, the spatial distributions of phytoplankton and zooplankton were uncoupled at taxonomic and functional levels with each responding to a different set of environmental drivers. The uncoupled biogeographies of plankton communities across boreal lakes indicate that taxon-specific and functional trait driven ecological interactions do not modulate large-scale spatial patterns of phytoplankton and zooplankton in a coordinated way.Our results indicate that forces beyond the phytoplankton-zooplankton trophic coupling are different, and more relevant for each trophic level : likely fish predation for zooplankton and resource levels for phytoplankton.

Keywords : plankton ; community ; functional traits ; Canada ; water quality ; habitat ; biogeography ; morphometry ; boreal

1.2 Introduction

In lakes, planktonic consumers (zooplankton) and primary producers (phytoplankton) interact strongly, mainly via trophic relationships (Porter, 1977; Sterner, 1989), and studies on trophic cascades have emphasized how changes at one trophic level can affect entire food webs (Carpenter *et al.*, 1985) . While top-down and bottom-up factors have typically been studied for their influence on standing biomass, they also influence species composition (McQueen *et al.*, 1989; Ghadouani *et al.*, 2003). Although many studies have investigated the taxonomic biogeography of zooplankton (Keller et Pitblado, 1989; Pinel-Alloul *et al.*, 1995; O'Brien *et al.*, 2004) and phytoplankton (Pinel-Alloul *et al.*, 1990; Stomp *et al.*, 2011) hlseparately, we know of only one small-scale study that examined the concordance between their taxonomic community structure across a suite of ponds (Soininen *et al.*, 2007).While the pond study did not find a significant spatial concordance between phytoplankton and zooplankton, one might expect that the trophic interactions between the two plankton groups should strongly constrain their respective compositions, especially when functional traits related to food web dynamics are considered. We hypothesize that phytoplankton and zooplankton joint biogeographies should be linked, especially when using a functional trait lens.

Biogeographical concordance between phytoplankton and zooplankton should be more observable for functional traits than for taxonomic groups for a number of reasons. Although zooplankton exhibit prey selectivity (e.g. Vanderploeg, 1981; Paffenhöfer, 1984), individual taxa generally feed on many different phytoplankton species (see Knisely et Geller, 1986). At the same time, because of the high functional redundancy among zooplankton species (Barnett *et al.*, 2007), is unlikely that spatially and temporally stable species-specific interactions will be common enough for the species composition of phytoplankton to be observably constrained

by any particular zooplankton species and vice-versa. On the other hand, at the ecosystem-level, grazing by Daphnids on edible phytoplankton in early seasonal succession leads predictably to a "clear-water phase" in lakes (Lampert *et al.*, 1986; Talling, 2003). Furthermore, other trophic interactions between specific functional groups of phytoplankton and zooplankton have been invoked as important drivers of other aspects of plankton succession (PEG model) in temperate lakes (Sommer *et al.*, 1986, 2012). Such repeatable patterns indicate that trophic interactions between plankton are likely stronger at a more coarse taxonomic resolution (e.g. *Daphnia* genus) and even more so at the functional level (e.g. small, edible phytoplankton). In other words, by controlling for functional redundancy between species by grouping them according to their function, stronger, repeatable patterns of interaction begin to emerge. Therefore, at the landscape level, we expect to observe tighter coupling between phytoplankton and zooplankton functional traits related to food web interactions than for taxonomic groups, observable in their respective biogeographies.

A significant coupling between the two plankton groups could also arise from similar responses to environmental drivers. The distributions of both phytoplankton (Pinel-Alloul *et al.*, 1990) and zooplankton (Keller et Pitblado, 1989) species respond to lake nutrient status, which could also result in a coupling of their distribution at the landscape scale. However, beyond lake nutrient status, the response of both plankton to gradients of other environmental variables such as lake colour (dissolved organic carbon content), lake size and stratification is not clear. Furthermore, when considering a suite of environmental variables, different variables do not necessarily have the same spatial structure (Lapierre *et al.*, 2015). Consequently, while the two plankton groups will each respond to variation in their environment, we do not expect such responses to be coordinated across a suite of 5 different variable types. To that end, we considered two categories of en-

vironmental variables : proximal (i.e. water quality) which generally have a strong landscape spatial structure and habitat characteristics (i.e. morphometry) which have a weaker landscape spatial structure (Lapierre *et al.*, 2015).

In a metacommunity context, with respect to the relative roles of environmental drivers and dispersal distances between lakes, phytoplankton generally respond to environmental factors while zooplankton are more dispersal-limited (Beisner *et al.*, 2006; De Bie *et al.*, 2012; Padial *et al.*, 2014). The differential response patterns could also preclude biogeographic coupling of the groups. In sum, because of differential relative responses of phytoplankton and zooplankton to environmental factors and distances between lakes, we must control for their respective effects before assessing the effect of trophic interactions on the biogeographic coupling of the two plankton groups.

Here, we provide the first comprehensive study to directly consider the potential for trophic interactions between planktonic organisms to affect the coupling of their biogeographic distributions. We expected weaker coupling at the taxonomic level, but stronger coupling when using a functional trait approach, which accounts more mechanistically for trophic interaction potential via the selection of functional traits related to food web responses : to resource availability (phytoplankton), feeding behaviours (zooplankton), and predator evasion (phytoplankton and zooplankton).

1.3 Materials and Methods

1.3.1 Study lakes and sampling

Crustacean zooplankton samples were collected from 104 lakes with a low level of anthropogenic disturbance, within three environmentally (Figure 1.1, Table 1.1) and geologically (see Roy, 2012) distinct regions of Quebec, Canada, during

Tableau 1.1 Means (standard error) and ranges of environmental variables : water quality (WQ), and morphometry (M) with the number of missing values (NA) and the transformation used.

Variable (abbreviation)	Category	Units	Mean (se)	Range	#NA	Transfo.
Chlorophyll*a* (chl*a*)	WQ	µg/L	1.7 (0.2)	0.2-11.6	0	$\log_{10}$
Total Phosphorus (TP)	WQ	µg/L	10 (0.7)	2.9-45.0	0	$\log_{10}$
Total Nitrogen (TN)	WQ	mg/L	0.21 (0.01)	0-0.6	0	$\log_{10}$
Dissolved organic carbon (DOC)	WQ	mg/L	6.6 (0.4)	1.4-20.3	2	$\log_{10}$
Colored dissolved organic matter (CDOM)	WQ	1/m	2.6 (0.2)	0.01-17.2	1	$\log_{10}$
pH	WP		7.1 (0.08)	4-9.2	1	-
Water temperature (Twater)	WQ	°C	17.8 (0.3)	10.3-23.8	1	-
Maximum depth (Zmax)	M	m	7.9 (0.6)	1-30	0	$\log_{10}$
Lake Area (Area)	M	m^2	$8.2x10^7$ ($4x10^7$)	$1x10^3$ – $4x10^9$	0	$\log_{10}$

the years 2010 (Abitibi, May to October), 2011 (Chicoutimi, June to October) and 2012 (Schefferville, July to August). Integrated zooplankton samples were collected from the deepest point of each lake using a conical plankton net (110µm mesh, 0.30 m mouth diameter), equipped with a flow meter (General Oceanics, USA), hauled vertically from 1 m above the sediments to the surface. Zooplankton samples were anaesthetized using carbonated water and were preserved in 75% (final concentration) ethanol. In a subset of 48 lakes the phytoplankton community was also simultaneously sampled over the photic zone (in average 92% of lake depth) using a flexible PVC sampler tube and an integrated subsample (250 ml) was preserved in Lugol's solution.

Crustacean zooplankton were identified at the species level (but aggregated for

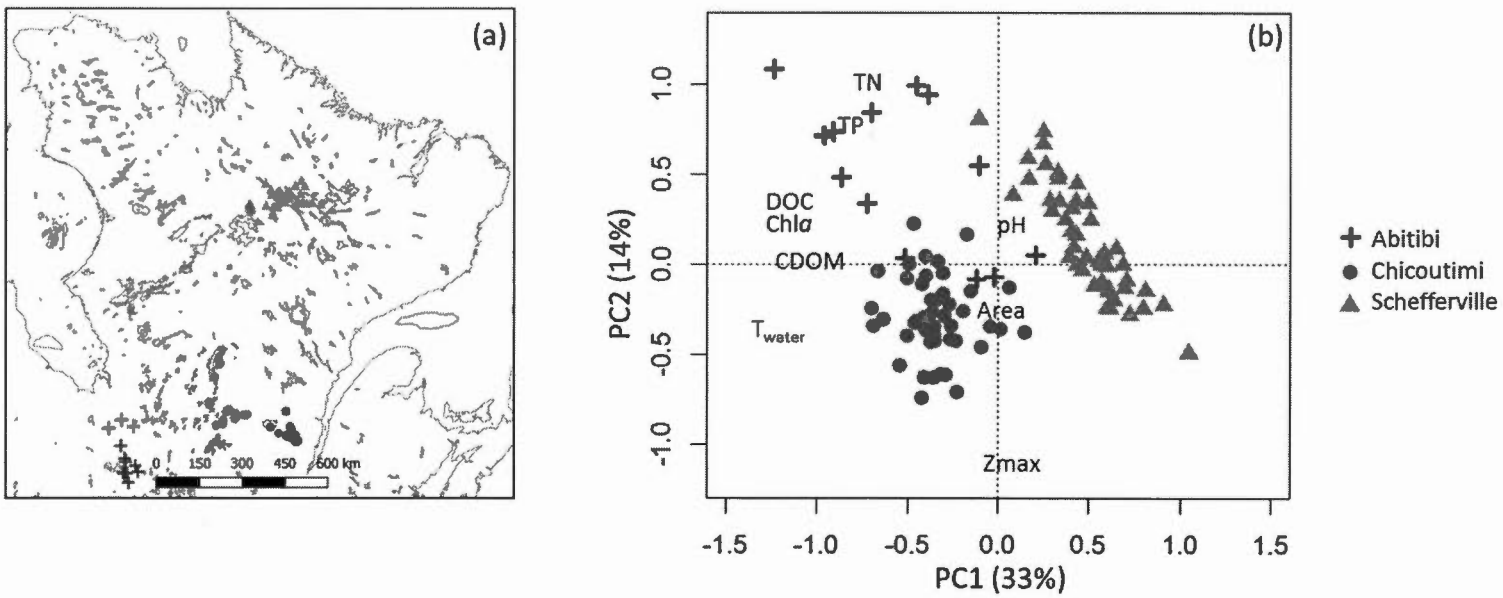

Figure 1.1 (a) Map of sampled lakes across three regions of boreal Quebec, Canada. (b) Lakes environmental principal component analysis (PCA) based on water quality and morphometric variables where the different symbols represent the three sampled regions. Zooplankton samples were collected in all lakes (n=108), while phytoplankton samples were collected in a subset of lakes (n=48). Abbreviations are as follows total phosphorus (TP) ; total nitrogen (TN) ; dissolved organic carbon (DOC) ; chlorophyll a (Chla) ; coloured dissolved organic matter (CDOM) ; water temperature (Twater) ; lake maximum depth (Zmax) ; lake area (Area).

analyses at the genus level to correspond to the phytoplankton data), using an inverted microscope (50-400X) and individuals were counted until a total of 200 individuals had been enumerated. For each taxon present in a lake, the length of 20 mature individuals was measured and biomass by taxon was estimated using length-dry-mass regressions (McCauley, 1984; Culver *et al.*, 1985). Phytoplankton were enumerated at the genus level using the Ütermohl method on an inverted microscope at 400X magnification. Phytoplankton biomass was estimated from biovolume computed using cell and colony length measurements and corresponding geometric forms (Hillebrand *et al.*, 1999). We also measured key limnological variables to characterize the lake and catchment environments. We used a multi-parameter sonde (YSI, Yellow Springs Instruments, OH, USA) to measure pH (at 0.5m) and temperature (at 0.5m, then averaged over the water column). Water samples were collected at 0.5m to measure the concentration of chlorophyll a (Chl*a*), total phosphorus (*TP*), total nitrogen (*TN*), dissolved organic carbon (*DOC*) and colored dissolved organic matter (*CDOM*). Chl*a* was extracted with 90% hot ethanol and absorption was measured spectrophotometrically before and after acidification to account for phaeophytin (after Nush, 1980; Lorenzen, 1967); *TP* was measured from water samples using the molybdenum-blue method following persulfate digestion (Cattaneo et Prairie, 1995); *TN* was measured using nitrates after persulfate digestion; *DOC* concentration was measured on an O.I. Analytical (Texas, USA) TIC/TOC using 0.45um filtered water after sodium persulfate digestion; *CDOM* was measured using a UV/Vis UltroSpec 2100 spectrophotometer (Biochrom, Cambridge, UK) at 440 nm. Missing values (see Table 1) were imputed using an approach based on random forest (missForest R package Stekhoven et Bühlmann, 2012, NRMSE : 0.038). Lake area was derived using ArcGIS V10 software (ESRI Inc., Redland, CA, USA). To visualize environmental differences between the three regions, we used a principal component analysis (PCA) using the rda function () (vegan R package Oksanen *et al.*, 2015).

Finally, because our sampling was discontinuous on the landscape we used the Euclidian distance between lakes to characterize the effect of dispersal limitation on the distribution of taxa and functional traits.

1.3.2 Functional trait composition and diversity

Given that our objective was to test for a significant coupling between adjacent trophic groups, we selected functional traits (Table 1.2) that explicitly translate to feeding interactions between phytoplankton and zooplankton, and how they interact with other trophic levels in the wider food web. For phytoplankton, we selected traits that define how they interface with resources (i.e. nutrients and light) and their predators (motility, edibility, colony formation). For zooplankton, we focused on traits that define how they consume phytoplankton (i.e. feeding type and trophic group). Phytoplankton trait values were obtained from a literature review (see Longhi et Beisner, 2010, for details)and included (i) capacity for N-fixation, (ii) silica demand, (iii) capacity for mixotrophy, (iv) pigment composition (v) cell motility and (vi) edibility to zooplankton (<35µm maximum linear dimension) and (vii) tendency to form colonies. Crustacean zooplankton traits values were also obtained from a literature review (see Barnett *et al.*, 2007) and included (i) feeding type and (ii) trophic group. For both zooplankton and phytoplankton, we also used the average individual biomass of each taxon as an integrative functional trait of body size (Brown *et al.*, 2004; Litchman *et al.*, 2013) related both to resources acquisition and predation avoidance (Table 1.2).

1.3.3 Statistical analyses

To visualize how phytoplankton and zooplankton taxa and traits were distributed on the landscape, we used their percentage of occurrence lakes sampled. To compare the distribution of abundant and rare phytoplankton and zooplankton,

Tableau 1.2 Phytoplankton and zooplankton functional traits used in this study.

	Category	Traits	Values
Phytoplankton	Resource acquisition	Nitrogen Fixation	yes/no
		Si requirement	yes/no
		Mixotroph	yes/no
		Pigments	Green Blue Brown Mixed
	Predation avoidance	Motility	None F(Flagellated) V(Vacuole)
		Edible	yes/no
		Colonial	yes/no
Zooplankton	Resource acquisition	Trophic position	Carnivore Omnivore-Carnivore Omnivore Omnivore-Herbivore Herbivore Immature
		Feeding type	B (*Bosmina*)-filtration C (*Chydorus*)-filtration D (*Daphnia*)-filtration S (*Sidae*)-filtration S Stationary Suspension S Raptorial

we used the relationship between the ranked occurrence and the log mean density of each taxon in lakes over the three regions. We then tested for differences in taxonomic or functional composition between the three regions using a Canonical Analysis of Principal Coordinates (CAP Anderson et Willis, 2003, BiodiversityR package), a constrained ordination technique. Using the CAP leave-one-out allocation success (Anderson et Willis, 2003) we assessed the distinctness of regional compositions using the proportion of correct allocation, which can be interpreted as the strength of the compositional differences between regions. Prior to the CAP ordination, taxonomic composition was Hellinger-transformed to reduce the effect of double zeroes.

To test whether the distributions of phytoplankton and zooplankton communities were coupled across the landscape, we used a hierarchical framework (Figure 1.2). First, we tested for significant coupling between the composition of the two groups at the taxonomic and functional trait levels using a Procrustes analysis. Specifically, we tested the degree of concordance between the PCA ordinations of phytoplankton and zooplankton taxonomically-defined communities. For lake communities defined by traits, we compared the lake weighed centroids determined using Principal Coordinates Analysis (PCoA) and the dbFD function (FD R package, Laliberté *et al.*, 2014). We tested the significance of the Procrustes statistic using a permutation procedure (9999 simulation, protest function in vegan R package, Oksanen *et al.*, 2015). To further investigate whether the coupling could be explained by a similar response of the two groups to environmental variables or by limitation to dispersal (see Figure 1.2) we also tested for a significant coupling after controlling for environmental factors (water quality characteristics and morphometry) and space (using latitude and longitude coordinates) using an RDA (see next section).

To directly evaluate the relative importance of environmental and spatial variables

as drivers of the taxonomic and functional composition of phytoplankton and zooplankton, we used distance-based redundancy analysis for taxonomic composition (dbRDA, Legendre et Legendre, 1998) and multiple regression for each functional trait both followed by variation partitioning (Borcard *et al.*, 1992). We separated the environmental variables into two groups; water quality (WQ, i.e. *chla*, *TP*, *TN*, *DOC*, water color, pH, temperature) and morphometry (M, i.e. lake area and depth). Prior to the RDAs and multiple regressions, we used a stepwise selection (based on AIC) of variables within each group of environmental variables. We identified variation that was shared between the two groups of environmental variables (WQ+M), and variation that was shared between environmental variables and space (S) : WQ+S and M+S, enabling the determination of whether environmental variables were spatially structured. Finally, to visualize the relationship between phytoplankton and zooplankton taxa and functional traits, we used a redundancy analysis (rda in vegan R package, Oksanen *et al.*, 2015) with all the taxa and all the functional traits combined.

1.4 Results

1.4.1 Biogeographical patterns

Based on our set of environmental variables, we observed important environmental differences between the three regions (Figure 1.1). The first principal component mainly differentiated the Abitibi and Chicoutimi regions from Schefferville. The difference was mainly related to temperature, productivity and water quality (i.e. variables with a strong loading on the first PC). The second axis was mainly related to lake morphometry and nutrient concentration, and differentiated the Chicoutimi region from Abitibi (Figure 1.1). Lakes in the Schefferville region were spread across the second axis.

The average percent occurrence of phytoplankton taxa in lakes (Figure 1.3a) was

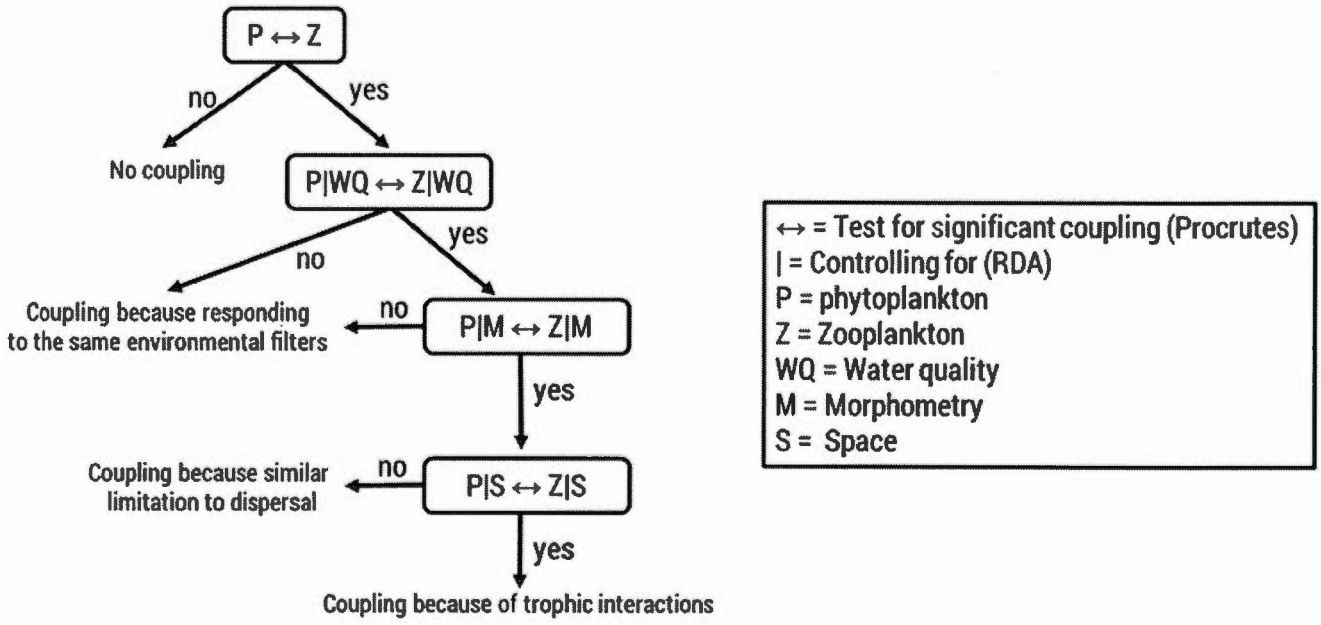

Figure 1.2 Conceptual framework used to test for a significant coupling between zooplankton and phytoplankton communities using taxonomy and functional traits, while controlling for environmental factors (water quality WQ, morphometry M) and dispersal limitation (space S).

24% for phytoplankton taxa (median 15%) and 21% for zooplankton taxa (Figure 1.3b, median 8%). Five phytoplankton taxa *Mallomonas* (94%), *Cryptomonas* (88%), *Dinobryon* (83%), *Anabena* (65%) and *Asterionella* (63%), were observed in more than 60% of lakes. For zooplankton *Leptodiaptomus* (89%), *Daphnia* (87%), *Bosmina* (84%) and *Holopedium* (64%) had occurrences greater than 60%. Of the 56 phytoplankton taxa, 34 (61%) were observed in all three regions, while across all 27 zooplankton taxa, 10 (37%) were observed in all regions. For phytoplankton, the relationship between mean local biovolume and ranked occurrence was not significant, while for zooplankton mean local biomass decreased along ranked lake occurrence (Figure 1.3). The differences in taxonomic composition between regions were less important for phytoplankton (CAP ordinations : 69%, p=0.01, Figure 1.4a) than for zooplankton (76%, p=0.01, Figure 1.4b).

For both phytoplankton and zooplankton, all functional traits were present in all three regions. All phytoplankton functional traits occurred in more than 90% of lakes, with the exception of two traits associated with cyanobacteria : presence of a vacuole for motility (63% of lakes) and the potential to fix nitrogen (58%). The occurrence of zooplankton functional traits ranged between 18% for carnivores and omnivore-herbivores, and 100% for herbivores, with the average occurrence of zooplankton traits being 64% (median 75%). Functional composition between regions did not differ for either phytoplankton, nor zooplankton (35%, p=0.69 and 49%, p=0.15 respectively, Figures 1.4c and 1.4d). In the taxonomic and functional Procrustes analyses (see 1.2) we found a significant correlation between phytoplankton and zooplankton genera, but the correlation was not significant after controlling for water quality, morphometry or space using an RDA. For functional traits, we observed no significant correlation before or after controlling for environment and space.

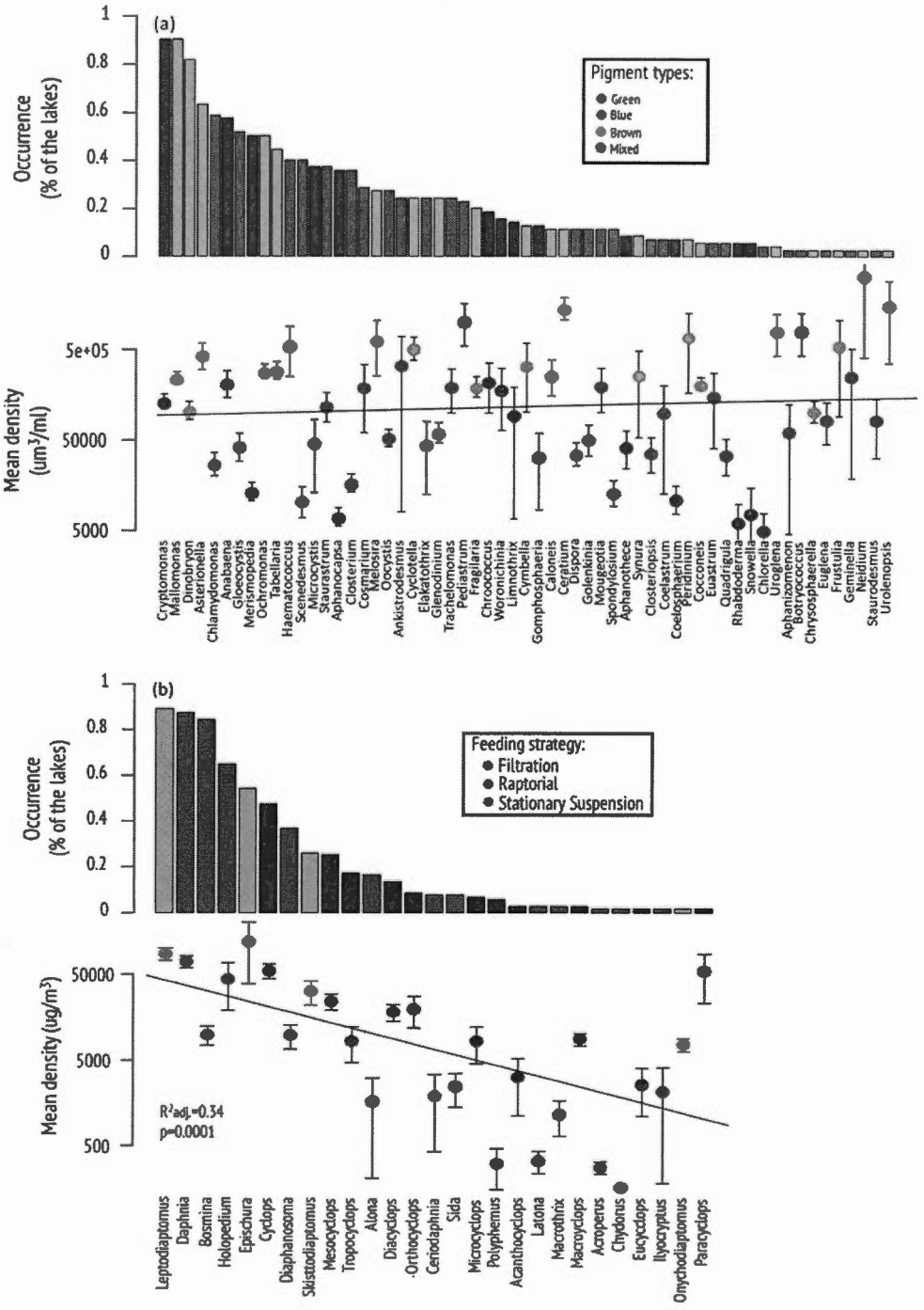

Figure 1.3 Ranked occurrence (percent of all lakes) and mean density (average biomass per lake) of (a) phytoplankton and (b) zooplankton taxa. Error bars represent the standard error of mean density. Bars and dots were coloured by Pigment trait type for phytoplankton and the Feeding strategy trait for zooplankton.

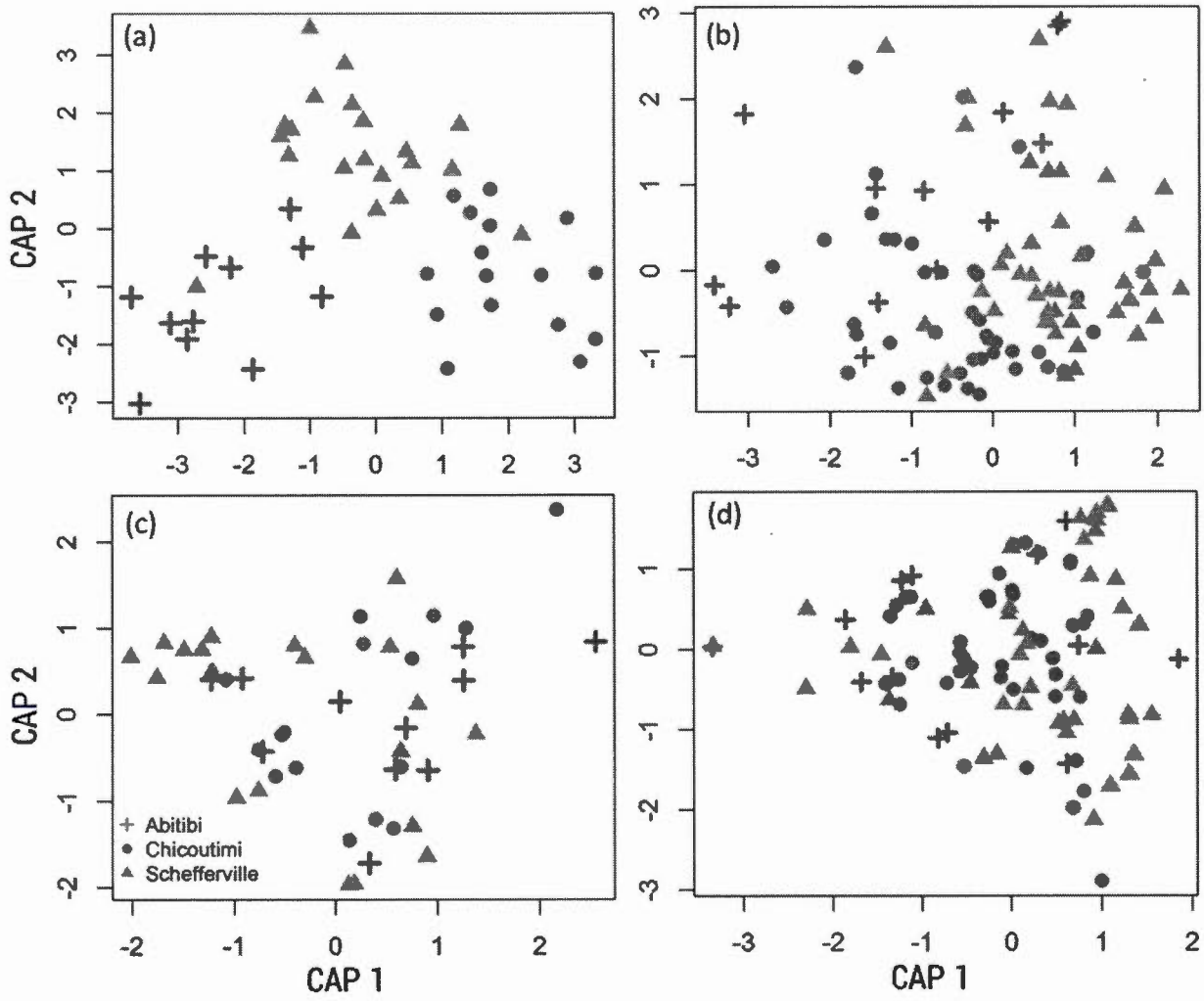

Figure 1.4 Two-dimensional scatter plot of canonical axes of the CAP ordinations for (a) phytoplankton and (b) zooplankton taxonomic composition and their respective functional trait compositions (c, d). Symbols represent the different regions. Strong regional differences occurred for taxonomic composition of phytoplankton (a, p=0.01) and zooplankton (b, p=0.01), but were not significant for functional trait composition (c and d).

1.4.2 Factors related to community composition

The RDA model explained 4% of the variation in phytoplankton taxonomic composition. For functional traits, multiple regression explained up to 27% of variation in the proportion of the different functional traits (Figure 1.5a), but no variation associated with the distribution of mixotrophy, non-motility, nor biovolume. Phytoplankton functional trait variation was not related to spatial factors, but a shared component between water quality and spatial factors indicated that water quality variables were spatially structured. Water quality variables were most consistently explanatory factors of the phytoplankton functional traits for which variation was explained (blue bars; Figure 1.5a). The exceptions were the flagellated trait, which responded to lake morphometry, and the mixed pigment trait for which variation was shared between water quality and morphometry.

After forward selection, the RDA of phytoplankton composition was constrained by *TP*, *CDOM*, pH and lake area (Figure 1.6a). Based on the first axis, differences in taxonomic composition could be mainly explained by lake nutrient status and coloured carbon content. Similarly, for traits (Figure 1.6c) functional composition also responded to lake temperature, nutrient status and carbon content according to the first axis. Functional traits related specifically to *cyanobacteria* (Pigment blue, N fixation and Motility-V) were positively associated with the first axis while traits (Pigment ands mixed brown, Si requiring, Motility-F) related to other key taxonomic groups (including *chrysophytes*, *cryptophytes* and *diatoms*) were negatively associated with that primary axis. In the taxonomic and functional RDA, the first two axes were significant.

For zooplankton, the global RDA models explained 11% of the variation in taxonomic composition (Figure 1.5b), and between 6% and 32% of the variation in the proportion of different functional traits (Figure 1.6d). Similar to phytoplank-

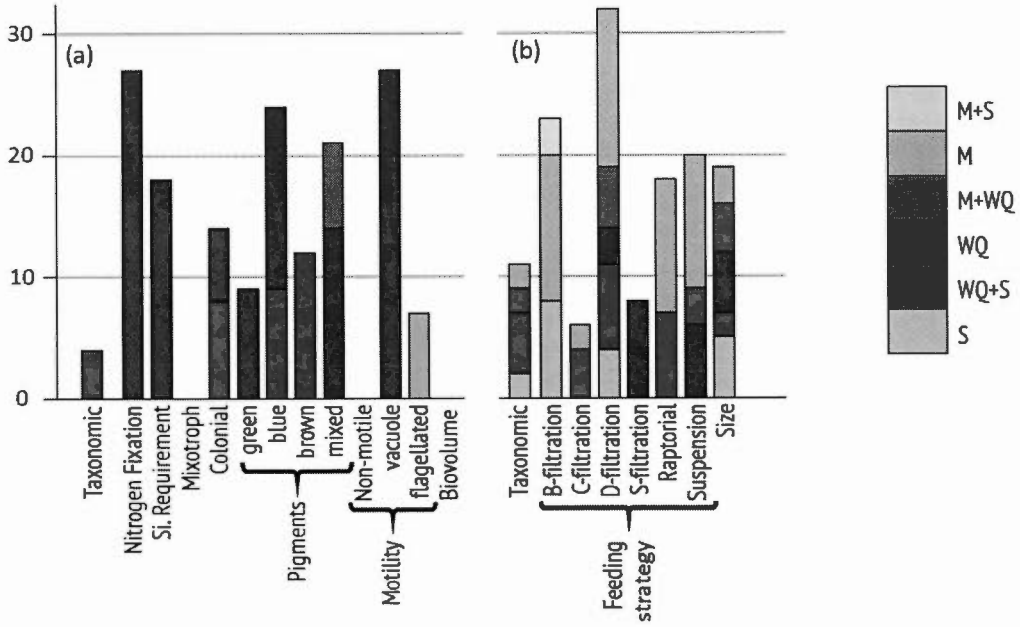

Figure 1.5 Variation explained (adjusted R2) by environmental and spatial factors for (a) phytoplankton and (b) zooplankton taxonomic composition and each functional trait. Only regression and RDA models that were globally significant are displayed. The variation that was independently explained by a group of variables is represented if significant, and shared variation represents the sum of variation shared between any of the groups of variables, represented with a +. Abbreviations are as follows : morphometry (M) ; water quality (WQ) ; space (S).

ton variation was shared between water quality and space, but spatial factors also independently explained a significant portion of the variation in zooplankton taxonomic composition, B-filtration, D-filtration and size. For taxonomic composition and most functional traits, a large portion of the variation was explained by lake morphometry (yellow bars; Figure 1.5b). However, for most traits and taxonomic composition, some variation was either shared or explained independently by water quality.

In the subsequent RDA of zooplankton taxonomic composition, constrained by morphometric and water quality variables (Figure 1.6b), variables related to lake productivity loaded on the first axis, while variables relate to lake morphometry (lake depth and area) loaded more strongly on the second axis. For functional traits (Figure 1.6d), the first axis was mainly related to lake depth, with the second being related to lake area. The raptorial feeding trait was highly correlated with deep lakes and B-filtration with large lakes while D-filtration was related to large and deep lakes. C-filtration was negatively related to depth, and positively with lake area, while stationary suspension was negatively related to both. In the taxonomic and functional RDA, the first two axes were significant.

1.5 Discussion

1.5.1 The distribution of taxa on the landscape

While there were some commonalities in the distributions of phytoplankton and zooplankton taxa, including the tendency to include both ubiquitous and rare genera (observed in fewer than 20% of lakes), we also observed many important disparities at the landscape scale. Typically, taxa that occur in many sites on a landscape are also locally abundant, while rare taxa tend to have comparatively low local abundances (reviewed in Brown *et al.*, 2006). In our study, zooplankton taxonomic distributions followed this general pattern. In contrast, the landscape

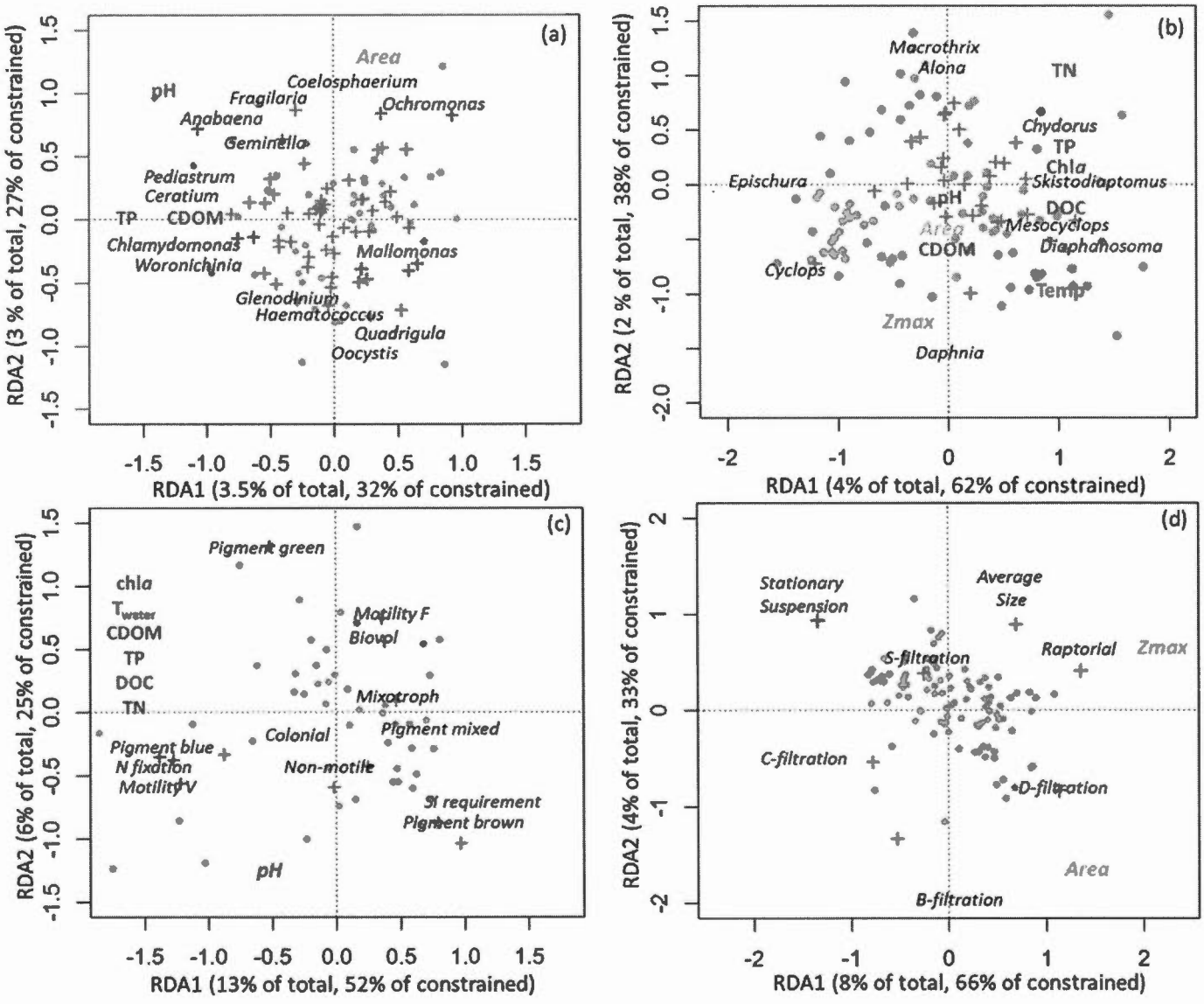

Figure 1.6 RDA ordination triplots of the (a, c) phytoplankton and (b,d) zooplankton composition classified by (a,b) taxonomy and (c,d) functional (c, d) traits. The RDA was constrained by variables related to water quality and by variables related to lake morphometry. Taxa and functional trait response variables are represented by crosses, and environmental explanatory variables by arrows. In the taxonomic RDAs (a, b), only taxa with loadings over 0.20 are displayed. Abbreviations are as follows total phosphorus (TP); total nitrogen (TN); dissolved organic carbon (DOC); chlorophyll a ($Chla$); coloured dissolved organic matter ($CDOM$); water temperature ($Twater$); lake maximum depth ($Zmax$); lake area ($Area$)

distribution of phytoplankton taxa was different, and comparably invariant, along a gradient from high to low regional occurrences. Many phytoplankton taxa with low occurrence (regionally rare), had high local biomass when present. Hence, phytoplankton taxa seem to maintain a consistent regional biomass by either being modestly abundant in many lakes, or by achieving particularly high local abundance in the few lakes in which they are found. Although dispersal limitation has been used to explain weak similar relationships between species density and occurrence in previous work (Blackburn *et al.*, 2006), a similar explanation should not apply here, as phytoplankton are generally more efficient dispersers than zooplankton (De Bie *et al.*, 2012).

1.5.2 Regional differences in composition and environment

We observed important differences in phytoplankton and zooplankton taxonomic composition between the three regions, which indicates that environmental differences and/or dispersal limitation were important drivers of the distribution of plankton taxa at the regional scale. In contrast, functional composition did not differ among regions, indicating that the environmental heterogeneity and/or the distance between the three regions was not important enough to prevent any functional traits from being distributed across the whole landscape. However, this latter biogeographic response does not mean that functional composition was similar across all the lakes. Environmental factors explained an important amount of the variation in most of the functional traits (Figure 1.5), indicating that the control of functional composition is acting at smaller spatial scales. We also observed that the control by lake characteristics (water quality and morphometry) of plankton taxonomic and functional composition is far more important than is the effect of dispersal limitation. Furthermore, our results support the earlier results of Beisner *et al.* (2006) across a much smaller lake landscape, that the dispersal limitation of zooplankton (including functional traits here), was a more important

community structuring feature than it was for phytoplankton.

1.5.3 Divergent responses of phytoplankton and zooplankton to their environment

Although both groups responded strongly to environmental factors in general,they both responded to a different environmental variable type. Phytoplankton taxonomic and functional trait compositions responded most consistently and strongly to water quality (i.e. their proximal environment). Such responses were expected at the taxonomic level (Watson *et al.*, 1997),interestingly the response was similar at the functional level. On the other hand, while zooplankton composition responded strongly to lake morphometry, lesser effects of water quality were also evident, suggesting an integrated response. The response of zooplankton to water quality could either occur directly, or indirectly via the trophic link to phytoplankton. For morphometry, the response could also result directly from characteristics of their habitat such as a change in lake physics. However, it is more likely to be an indirect trophic effect of fish predation, as previously observed relationships between zooplankton composition and lake morphometry have been attributed to the effect of lake morphometry on fish presence (O'Brien *et al.*, 2004). In particular, lake depth influences fish community composition (Jackson et Harvey, 1989), with larger lakes tending to have longer food chains (Post *et al.*, 2000), thereby modulating the trophic cascade effect on zooplankton through planktivore fish feeding (Carpenter *et al.*, 1985). The responses we observed in the variation explained in zooplankton taxonomic composition and functional traits could thus be related to local variation in fish composition (data which we did not have). This may also explain why the proportion of D-filtration was higher in larger lakes, as the presence of an extra trophic level (total of 4-levels) may decrease fish planktivory, resulting in less top-down pressure on large herbivorous Cladocera, which are preferred prey for fish. Planktivorous fish could in this way be more abundant

in shallow lakes and exert stronger control over Daphnid abundances in a way that corresponds with our results. Repercussions through the community were observable in Figure 1.6d, with reductions in D-filtration leading to an increased proportion of stationary suspension herbivory, dominated by Calanoid copepods. Also, the relative biomass of the C-filtration group was negatively related to lake depth, consistent with the fact that most species within this functional feeding type are littoral species and shallow lakes contain greater proportion of habitats that are littoral.

1.5.4 Uncoupled biogeographies of phytoplankton and zooplankton

Despite our initial hypothesis, the functional biogeography of phytoplankton and zooplankton were not clearly related, nor coupled after controlling for environment and space. The significant coupling observed taxonomically, could either arise because both plankton groups responded to similar environmental factors, or because their response to environmental factors is mediated through trophic interactions. For example, the concordant taxonomic response by both groups to phosphorus (*TP*, Figure 1.6 a and b), indicates the possibility that the effects of phosphorus enrichment at the phytoplankton level triggers a response at the zooplankton level. But such links cannot be directly tested with an observational study such as ours. Meanwhile at the functional level, there was no significant coupling between phytoplankton and zooplankton, even before controlling for environment and space, which indicates that each group, in a functional sense, is responding to different sets of factors.

Persistent differences in dispersal limitation may further explain the uncoupled biogeographies of the phytoplankton and zooplankton. In support of this differential dispersal, we found that spatial factors explained no significant variation in phytoplankton taxonomic or functional trait composition, while the relationship

between spatial factors and zooplankton taxonomic composition and B-filtration and D-filtration functional traits was significant. Thus, as observed elsewhere at smaller spatial scales (Beisner *et al.*, 2006; De Bie *et al.*, 2012), persistent differences in dispersal limitation between the two groups, may explain the observed decoupling. However, the importance of spatial factors was small compared to the total variation explained by the environmental and habitat (i.e. morphometric) variables. Hence, dispersal alone is unlikely to be a sufficient explanation for uncoupled biogeographies over the long-term.

The goal of including functional traits was to assess whether biogeographical coupling would be more likely to be observed at a more mechanistically aggregated level of organismal differentiation. We selected functional traits that are directly implicated in the lake food web for interactions between phytoplankton and zooplankton and in resource acquisition. The fact that none of the biogeographies were coupled, in the absence of environmental variables, indicates that in addition to the taxon-specific disjunction expected, there are also functional disjunctures. Overall, our study indicates that other food web components such as fish predation (zooplankton) and resource availability (phytoplankton) should be considered are more proximate variables driving the biogeographies of each group, and that a concordance between the two plankton groups themselves should thus not be expected. In summary, even if phytoplankton and zooplankton are strongly connected trophically and are a major pathway for matter and energy in lakes, impacts based on taxonomic or functional compositional changes will probably be limited at the landscape scale.

1.6 Acknowledgments

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CHAPITRE II

MAGNITUDE AND REGULATION OF ZOOPLANKTON COMMUNITY PRODUCTION ACROSS BOREAL LAKES

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N.B. References cited in this chapter are presented at the end of the thesis

Scientific Statement

The transfer of energy and materials from primary producers to higher trophic levels in lakes plays a key role in the function of aquatic food webs, which, in lakes, is mediated by zooplankton. Although zooplankton production rates at the individual population scale are known to be strongly dependent on body size, population biomass, and water temperature, the drivers of production rates at the whole communities scale are not well understood. Here, we show that zooplankton community production in a wide range of boreal lakes is correlated to the same factors that control zooplankton production at the population scale, but that it is further modulated by additional lake and watershed properties that operate only at the community scale.

2.1 Abstract

A major outstanding question in plankton ecology is whether the regulation of zooplankton production at the community level follows the same patterns that have been observed for individual populations. We used a novel biochemical approach to estimate in situ rates of crustacean zooplankton community production in 83 boreal lakes, with the objective of identifying the main drivers of zooplankton production at the community level across the boreal landscape. Our results show that the relationship of zooplankton community production to average community body size, total biomass and temperature is comparable to what has been observed for individual populations. At the community level, however, there are additional drivers, including lake morphometry, and catchment properties, which further influence zooplankton production and which cannot be inferred from population level patterns.

2.2 Introduction

The transfer of energy and biomass from primary producers to higher trophic levels is central to the functioning of aquatic ecosystems. Zooplankton are the major trophic intermediary in lakes, and understanding the dynamics of material and energy transfer through aquatic food webs necessarily requires quantification of biomass production rates of zooplankton communities, and an understanding of factors regulating these rates. Notably, whereas both the magnitude and drivers of phytoplankton and fish production at the community level in north-temperate lakes have been extensively studied (Schindler, 1974; Vollenweider, 1976; Karlsson *et al.*, 2009; Benoit *et al.*, 2016), the magnitude and regulation of zooplankton community production have not. Traditional approaches to quantify zooplankton production are based on extremely labour-intensive and detailed temporal monitoring of cohorts of individual populations (see Downing et Rigler, 1984; Dolbeth et Cusson, 2012). Alternatively, approaches relying on biomass size spectra analyses (Sprules et Munawar, 1986; Sprules et Stockwell, 1995) can provide 'community-level' information on productivity and transfer efficiency, but these analyses often require prey size measurements and assume fixed (often relative) transfer efficiencies.

Cohort-based approaches yield estimates of production that apply only to the target populations, yet it is community production which is at the core of many ecological and trophic questions (e.g. Garcia-Comas *et al.*, 2016). For instance, quantitative evaluation of trophic interactions using productivity estimates for bacterial and primary producers (typically community-level measurements) require similar community-level zooplankton productivity measurements. Community production must be estimated individually on the basis of cohort analysis, rendering this population-based approach to community production difficult if not

impossible to implement across many lakes, especially in remote regions where repeated sampling is a challenge. It is for this reason that other studies have not measured actual population production rates, but instead have used available empirical models to estimate community production (Johannsson *et al.*, 2000; Stewart *et al.*, 2010; Kelly *et al.*, 2014; Mehner *et al.*, 2015) based on published models linking population production to population biomass, body size, and water temperature (Downing et Rigler, 1984; Shuter et Ing, 1997; Stockwell et Johannsson, 1997).

Whereas population-based approaches such as summed population estimates or population-based empirical models may provide reasonable estimates of community production, neither approach lends itself to exploring the regulation of zooplankton production at the community level across lakes and along environmental gradients. On one hand, it is difficult, if not impossible, to infer the factors regulating zooplankton production at the community-level on the basis of regulation of the individual populations composing the community, because at the community-level there may be additional drivers, such as those determining the partition of total biomass into the different populations, and ecological interactions between constituent populations (Gliwicz, 2009). On the other hand, it is unclear whether zooplankton production at the community-level follows scaling patterns relative to total biomass, mean body-size and temperature resembling those identified for the constituent populations. Plante and Downing (1989) demonstrated consistency in both the body size- and temperature dependencies of production across a wide range of invertebrate species, suggesting that a mixed community may indeed follow the general patterns of its component individual populations. This conclusion, however, is based on aggregating data across species across many orders of magnitude in body size, from rotifers to large benthic invertebrates; the pattern (Plante et Downing, 1989) appears to break down within narrower

ranges of body mass. In particular, there is evidence that for lake zooplankton, specific production (or production to biomass ratio; P/B) varies greatly across species (Banse et Mosher, 1980), and also through time and space within a single species (Downing et Rigler, 1984). The extent to which population-level metabolic scaling can be extrapolated to the community level is a question that is relevant not only to our understanding of lake plankton, but to other communities as well, including phytoplankton, invertebrates, and fish, and goes to the core of ecology, for example, underpinning the metabolic theory of ecology (Brown *et al.*, 2004).

Assessing the regulation and body-size scaling of zooplankton production at the community level therefore requires an independent quantification of total production rate that is not based on population-level estimates, and this across a variety of lakes and along sufficiently broad environmental gradients. Here we present a large-scale study of the magnitude and regulation of zooplankton community production, using a novel approach to quantify community-level crustacean zooplankton biomass production rates that does not involve extrapolating population-based empirical models. Our method is based solely on measurement of the standing activity and rate of decay of the crustacean moulting enzyme, chitobiase (Sastri *et al.*, 2013), which yields an integrative, short time scale, measure of community production rates that can be obtained relatively easily across many lakes. We applied this approach across a large suite of boreal lakes that span wide geographic and environmental gradients to determine : 1) the range in daily total crustacean production rates across lake gradients; 2) the mean body-size and temperature dependency of community production rates in comparison with those reported for individual zooplankton populations; 3) the main environmental drivers of short time scale zooplankton community production, and the most robust predictive models. We use these elements to develop an integrative scheme for zooplankton community production regulation across boreal lakes, combining

elements of zooplankton community structure and key environmental factors at the lake and catchment scales.

2.3 Materials and Methods

2.3.1 Study lakes and sampling

Daily total crustacean zooplankton production rates (ZP) were measured in 83 boreal lakes from three regions across Quebec, Canada (Figure 2.3,Table 2.1). Twelve lakes in the Chibougamau region (49.10-50.85 °N, 72.98-74.52 °W), and 27 lakes in the Chicoutimi region (47.78–48.77 °N, 71.13–72.12 °W) were sampled from 3 June to 2 October 2011. Some Chibougamau and Chicoutimi lakes were sampled up to three times (5 lakes three times and 7 lakes two times), with the temporal separation between these being sufficiently long (38-74 days) to assume novel environmental conditions and communities composed of different species or population cohorts at very different stages of seasonal development, and independent daily production estimates. A further 43 lakes were each sampled once in the Schefferville region (54.16–55.47 °N, 65.21–68.84 °W) in August 2012. Zooplankton communities were sampled using a 110 m mesh, 0.30 m mouth diameter conical plankton net with flow meter (General Oceanics, USA), hauled vertically from 1 m above the lake bottom. Net contents were anaesthetized in soda water and preserved in 75% ethanol (final concentration).

Daily biomass production rates were estimated from measurements of the standing native activity (CBA_{NAT}), and the measured turnover rate (T_{CBA}) of the crustacean molting enzyme, chitobiase (CBA), in the water column using samples collected at 2 m depth (following Sastri et al. 2013). We assumed that samples from 2-m depth captures both the portion of the community that carries out diurnal migration but which nevertheless leaves a moulting trace in the epilimnion, as well as the portion of the community that resides predominantly in the

Tableau 2.1 List of variables included in best subsets regression and SEM models. Variable types are indicated according to the following categories : R-response, S-community structure, L-limnological, C-catchment.

Variable (abbreviation)	Category	Units	Mean	Range	Transformation
Crustacean zooplankton biomass production rate (ZP)	R	mgC m^{-3} day^{-1}	3.22	0.32-15.3	log_{10}
Epilimnetic temperature (Temp)	L	°C	16.77	11.9-23.0	
Dissolved organic carbon (DOC)	L	mg L^{-1}	6.17	1.4-14.3	log_{10}
Chlorophyll*a* (chla)	L	µg L^{-1}	1.5	0.2-5.5	log_{10}
Total Phosphorus (TP)	L	µg L^{-1}	9.63	2.9-22.8	log_{10}
Mean individual body mass (Size)	S	µgC $individual^{-1}$	1.17	0.2-3.4	log_{10}
Maximum individual body mass (W_m)	S	µgC $individual^{-1}$	81.7	12-115	log_{10}
Zooplankton biomass (Biom)	S	µgC L^{-1}	132	3.3-1147	log_{10}
Lake Area (Area)	L	m^2	$7.4x10^7$	$1x10^3 - 4x10^9$	log_{10}
% wetland cover in catchment (WET)	C	%	1.4	0-41	Loggit
% forest cover in catchment (FOR)	C	%	74	0-100	Loggit

epilimnion, as observed elsewhere for similar lakes (Brosseau *et al.*, 2012) ; these estimates may nevertheless represent underestimates, especially in terms of migrating Chaoborus, which inhabit bottom waters and are seldom present in surface water during daytime, when samples were taken. Daily ZP represents the production rate of biomass attributable to all somatic growth for the entire developing (actively molting) crustacean zooplankton community (methods in SI). Total zooplankton biomass across the 105 to 2000 µm equivalent spherical diameter (ESD) size range was calculated from Laser Optical Plankton Counter measurements for each net sample (see SI). Mean individual body mass for the community was calculated as the product of abundance and the mid-point of mass within a size class summed across all size classes > 90 µm and divided by total abundance.

To explain cross-lake variation in ZP, we measured a suite of environmental variables (within-lake and catchment levels, Table 2.1). Mean epilimnetic temperature (°C) was estimated from a multi-parameter sonde (YSI, Yellow Springs Instruments) profiles.Samples for phytoplankton biomass (*Chla* ; µg L^{-1}), *TP* (µg

L^{-1}), and *DOC* (mg L^{-1}) were collected from 0.5 m depth using a Van Dorn bottle. In the lab, Chl*a* was extracted with 90% hot ethanol and measured spectrophotometrically before and after acidification (after Nush, 1980) ; *TP* was measured using the molybdenum-blue method following persulfate digestion (Cattaneo et Prairie, 1995) ; and *DOC* concentration was measured on an O.I. Analytical (Texas, USA) TIC/TOC using 0.45 µm filtered water after sodium persulfate digestion. Morphometric and catchment-level variables consist of lake surface areas derived using ArcGIS V10 and the National Topographic Data Base (NTDB) and estimated catchment forest and wetland cover (%) obtained from Geobase (Geobase, 2009).

2.3.2 Statistical analyses

To compare patterns in total daily crustacean production rates with those reported for individual populations, and in particular with the Plante and Downing (1989) model based on a compilation of species-specific production data, we first built a regression model containing similar variables : standing biomass, mean size and temperature (Table 2.2, model A). We also explored potential environmental drivers of ZP, using 'best subset regression' to identify the best models for a selected number of explanatory variables (Table 2.2, models B-G) based on the significance ($p < 0.05$) of both the overall regression, ranked according to AIC values, and the explanatory variables. Finally, we merged the community structure, environmental, and catchment-level variables (Table 2.2, model H). This sequential approach allowed the emergence of the best combined predictive ZP model.

We further explored the relationships between the various drivers of ZP using structural equation modeling (SEM Bollen, 1989; Shipley, 2002; Grace, 2006). This approach allowed us to : 1) assess whether environmental variables affected

ZP directly via growth rates, or indirectly via community structure (biomass and body size); and 2) to better delineate the complex relationships between environmental factors and ZP (Figure 2.2a). In SEM, coefficients for each variable are evaluated for significance while holding all other variables constant. Thus, the inclusion of biomass as a variable in the model allows to identify other variables that may influence ZP through their effect on zooplankton growth rates, rather than on standing stock. These environmental factors influencing growth rates directly are those having significant direct links to ZP. Environmental factors acting indirectly on ZP are those that are mediated by other proximal factors. We initially constructed a SEM that included the expected links between environmental factors, community structure and ZP based on what is known about factors that directly or indirectly affect zooplankton production in lakes (Figure 2.2a). To find the most parsimonious SEM that could explain our data, we used an iterative fitting procedure. At each step we either added or removed the link that resulted in the largest decrease in the overall model AIC with no effect on the R^2 of ZP. The fit of each SEM to our data was assessed using the comparative fit index (CFI) and the p-value of the robust chi-square (χ^2), where a significant SEM model is one having a p-value greater than 0.05, as the null hypothesis is that there are no significant differences between the SEM and the data. Variables with no direct or indirect path to biomass or ZP were removed from the final SEM. SEM analyses were carried out with the Lavaan package (Rosseel, 2012) in R version 3.03 (R Core Team 2013).

2.4 Results

Lakes varied widely in size, trophic status and temperature (Table 2.1). Zooplankton community biomass across all lakes ranged more than two orders of magnitude (3.3 to 1147 mg C m^{-3}). Mean individual body mass across the crustacean communities ranged from 0.17 to 3.36 µg per individual, while chitobiase-estimated

ZP varied between 0.31 and 15.29 mg C $m^{-3}d^{-1}$. The basic multivariate model using biomass, size and temperature as independent variables, analogous to that presented by Plante and Downing (1989; hereafter PD) for individual populations, performed poorly with our community-level data, explaining only 16% of ZP variation ('model A'; Table 2.2). While our temperature coefficient (0.05) was roughly similar to theirs (0.03), our body size coefficient was not only different in magnitude (0.05) but also in sign (positive) in our model relative to PD's population-based annual estimate (-0.16). Although the general cross-lake trends derived from the PD model agreed with those of our ZP estimates (Figure 2.1, r=0.53, p«0.001), the PD model systematically overestimated community ZP on average (Mean Absolute Error = 1.6 mg C m-3 day-1, an overestimation of 70% on average) .

Best subsets regression yielded six models (Table 2.2, models B-G), and the best of the 1 to 3-variable models were selected using AIC. The best single-variable models (BC) included temperature and lake area, and were almost equivalent, both describing 12% of ZP variation. The best 2-variable models (DE) included either lake area and temperature, or lake area and Chla, both explaining 26% of total variation in ZP. The best 3-variable models (FG) incorporated temperature or TP to the previous models, explaining 31-32% of ZP variation. Inclusion of zooplankton standing biomass and mean size with the environmental variables (H) further improved the model fit (AIC=17) explaining 37% of ZP variation. Finally, the best predictive model (I) further included % wetland in the catchment ($R^2_{adj} = 43$ %, Table 2.2).

The final SEM (Figure 2.2b) was significant (p-value = 0.24, $\chi^2 = 25$; df= 21, CFI=0.99) with significant coefficients (all (p-values <0.05, see Table 2.4) for each relationship. As expected, ZP was positively related to total biomass, and also negatively related to mean body size. The distal (watershed and lake morphometry)

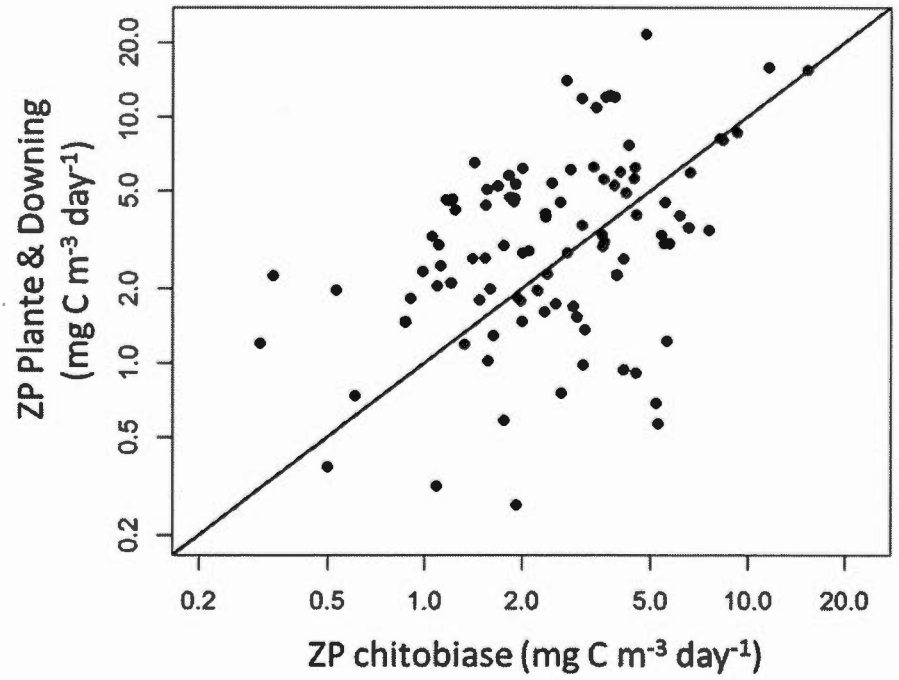

Figure 2.1 Comparison of zooplankton production using the PD (Plante and Downing, 1989) model and zooplankton production estimated using chitobiase. The 1 :1 line is shown on the diagonal.

Tableau 2.2 Regression models describing variation of crustacean zooplankton biomass production rates (ZP) in relation to environmental and community structure factors across all study lakes (n=99).

Model	Equation	R^2_{adj}	AIC
A	$ZP = -0.88 + 0.15\,Biom + 0.05\,Size + 0.03\,Temp$	0.16	44.26
B	$ZP = -0.27 + 0.04\,Temp$	0.12	47.2
C	$ZP = 0.97 - 0.09\,Area$	0.12	46.4
D	$ZP = 0.30 - 0.10\,Area + 0.04\,Temp$	0.26	30.7
E	$ZP = 0.98 - 0.10\,Area + 0.42\,Chla$	0.26	30.1
F	$ZP = 0.98 - 0.09\,Area + 0.39\,TP + 0.04\,Temp$	0.32	23.6
G	$ZP = 0.98 - 0.10\,Area + 0.30\,Chla + 0.03\,Temp$	0.31	24.1
H	$ZP = 0.64 + 0.24\,Biom - 0.23\,Size + 0.03\,Temp - 0.11\,Area + 0.34\,Chla$	0.37	17.7
I	$ZP = -1.41 + 0.25\,Biom - 0.25\,Size + 0.03\,Temp + 0.38Chla - 0.09Area - 0.18WET$	0.43	9.0

and proximal (lake chemistry, temperature) drivers exerted their influence on ZP indirectly, through their effect on zooplankton biomass and body size, and in some cases, also directly, the latter suggesting direct effects on zooplankton performance and growth for any given biomass or body size. The influence of in-lake variables (DOC, TP and temperature) on ZP was mainly mediated through their effects on *Chla*, although temperature also influenced ZP both directly and through an effect on mean body size. The distal drivers, led by % forest in the catchment (%FOR) exerted their influence on ZP through their effect on biomass and mean body size, as well as on in-lake variables, although %WET and lake size were also directly related to ZP and their direct effect was much more important compared to their indirect effects (Table 3). The overall (direct and indirect) effect size of all environmental factors on ZP together was larger (positive 0.98 and negative -0.70; Table 2.3) than the effect size of community biomass and size alone (positive 0.34 and negative -0.24; Table 2.3). The SEM also demonstrated additional interactions between standing biomass and body size and DOC and TP.

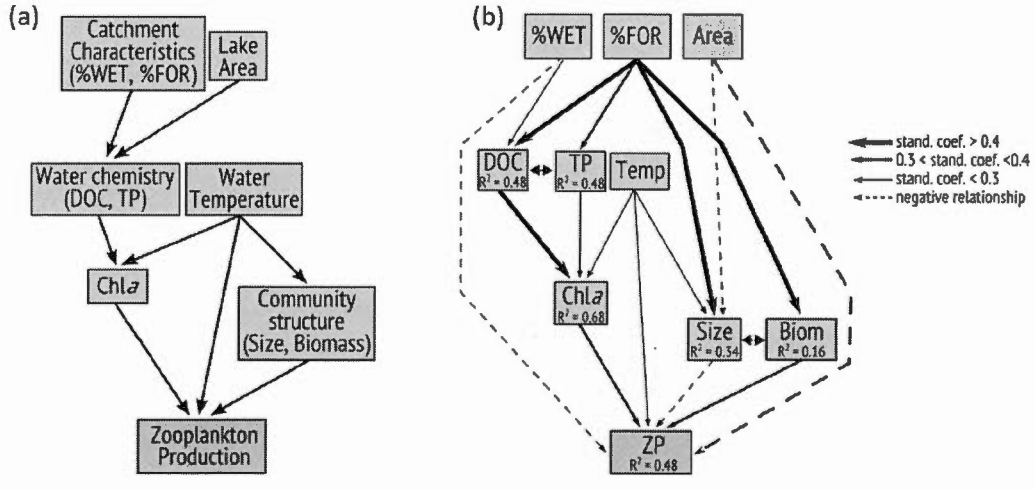

Figure 2.2 (a) Schematic diagram of the SEM model specified to include direct and indirect relationships between environmental variables and ZP, and (b) the final SEM ($X^2 = 9.2$; $p = 0.68$) describing variation in zooplankton production rate as a function of environmental variables and zooplankton community structure. Standardized coefficients are indicated on the arrows. Solid arrows indicate positive relations and dashed arrows indicate negative ones; the boldness of the arrow is related to the coefficient size..

2.5 Discussion

There was a surprisingly large range in total daily crustacean zooplankton production rate estimates across sampled boreal lakes, especially considering that most of lakes were oligo- to mesotrophic. Interestingly, while total biomass also varied greatly across lakes, it was by itself a very poor predictor of daily production, suggesting much variability in biomass-specific production across communities. Previous studies of zooplankton in lakes had reported large differences in daily and annual total crustacean production estimates across individual populations, even within the same lake, with both temperature and body size playing major determinant roles (Banse et Mosher, 1980; Downing et Rigler, 1984). Plante and Downing (1989; PD model) further demonstrated that these factors are consistently important across a wide range of aquatic invertebrate species based on empirical relationships, yet no study had tested whether these scalings hold at the community-level itself. Our enzymatic approach allowed us to obtain an independent estimate of total daily crustacean production rate that does not rely on population level estimates, and which reflects shorter frames than the latter, more comparable to the scales of variability in the main environmental drivers. Although the enzymatic assay has been itself calibrated using individual, species-specific growth increments, the relationship between enzyme activity and biomass production is consistent across crustacean groups (Sastri *et al.*, 2009,0), such that the total enzymatic activity (and its turnover) measured in a given water sample offers an integrative quantification of the total daily zooplankton production rate.

Our results confirm that while community estimates of daily zooplankton production rate are also dependent on body size and temperature, these dependencies are strongly modulated, and sometimes masked, by several environmental factors appearing to act only at the community level. The direct temperature dependency

of ZP was lower than in the PD model, with the direct body size dependency (Model A, Table 2.2) being positive, and opposite to allometric expectations (MTE, Brown *et al.*, 2004). However, after accounting for a suite of environmental factors, including Chla, lake size and catchment properties (Model I, Table 2.2), the resulting body size dependency ($M^{-0.25}$) became negative, as previously found (Stockwell et Johannsson, 1997), and of the expected magnitude (Dickie *et al.*, 1987) ; the temperature dependency was also more in line with previous reports (Plante et Downing, 1989; Shuter et Ing, 1997) once accounting for additional environmental variables. It would thus appear that both temperature and mean size may integrate the effects of other environmental variables in boreal lakes, such that in order to isolate the temperature and size dependencies of ZP at the community level it is necessary to account for the effect of these environmental variables. From a mechanistic perspective, these results indicate that body size and temperature dependency of freshwater ZP is modulated by factors (food and other environmental conditions) that likely influence community composition, which then influences the body-size dependency and the response of zooplankton to temperature (Shuter et Ing, 1997). The influence of food availability on the body size dependency of ZP had been demostranted for marine copepods (Lin *et al.*, 2013), but was not considered in previous freshwater, population-based models, which may also explain why the apparent size dependency in the empirical PD model was lower than expected.

Our study identified novel environmental variables affecting ZP at the community level. In their compilation, Plante and Downing (1989) observed no influence of lake area on population-level annual production, while we observed a distinct influence of lake size, with greater ZP in smaller lakes. This discrepancy suggests that lake area acts only at the community level, perhaps influencing community composition or species interactions along a gradient of lake morphometry. Smaller

lakes are more likely to be fishless (Scheffer et Van Nes, 2007), resulting in greater invertebrate versus fish planktivory, with important impacts on zooplankton community composition (Brooks et Dodson, 1965; Hanazato et Yasuno, 1989). Compositional alteration can in turn lead to life history shifts affecting reproductive rates that modulate community ZP without necessarily being accompanied by altered mean community body size. We also found that ZP was greater in catchments with lower % wetland coverage. While we were unable to identify the intermediary in-lake variable underlying this relationship, it is well known that the presence of wetlands in the catchment strongly influences material loading to lakes, notably N, P and especially DOC (Dillon *et al.*, 1991), influencing water chemistry and concomitantly, the composition of phytoplankton (Prepas *et al.*, 2001). It is interesting to note that the wetland effect in the multiple regression models was not diminished by the inclusion of variables such as nutrients and total or colored DOC, indicating that this % wetland likely integrates several different processes influencing zooplankton community structure, not just water color.

The SEM approach revealed more of the interactions of environmental and biological variables shaping community ZP. As expected, the effect of within-lake variables on ZP was mainly mediated through food concentration *Chla*, although direct and indirect (through body size) temperature effects were apparent. Catchment % forest cover, a watershed level variable similar to % wetland, indirectly influenced ZP via both in-lake variables and community properties, likely represents the integration of several watershed processes influencing lake chemistry, resource availability and even physical structure that affect zooplankton community composition and interactions. Although the causal link to ZP is not clear, it is interesting that the standardized cumulative effect of catchment-level variables was similar to the cumulative effect of within-lake variables, emphasizing a role of catchment properties on regulating daily zooplankton production. Similarly, while

lake area and temperature mainly exerted direct effects on ZP, indirect effects were also apparent, operating through mean body size. Together, these results imply a complex regulation of daily zooplankton production at the community-level.

While the Plante and Downing (1989) population-based model applied to our community data yielded estimates that were greater than our measured ZP, the resulting patterns were still generally consistent with our community-level ZP observations (Figure 2.1). This would suggest that that the basic scaling of zooplankton production to biomass, body size and temperature is roughly comparable between the population and community levels. Our results further demonstrate, however, that community estimates capture an additional layer of cross-lake variability, which is at least in part explained by a set of integrative watershed and lake drivers that do not appear to operate at the population level. Our results clearly indicate that total daily crustacean production regulation should not be assumed to be simply the sum of of its constituents, and that regulation occurs through a complex interplay between community structure, lake and watershed properties.

2.6 Acknowledgments

We thank Katherine Velghe and Marilyne Robidoux for help in the lab and field. Funding from the Groupe de recherche interuniversitaire en limnologie et en environnement aquatique (GRIL) and the Québec Centre for Biodiversity Science (QCBS) is gratefully acknowledged. BEB and PDG acknowledge funding from the Natural Sciences and Engineering Research Council of Canada (NSERC) in the form of Discovery Grants and the Industrial Research Chair in Carbon Biogeochemistry of Boreal Aquatic Systems (CarBBAS) co-funded by Hydro-Québec to PDG.

2.7 Supplementary Material

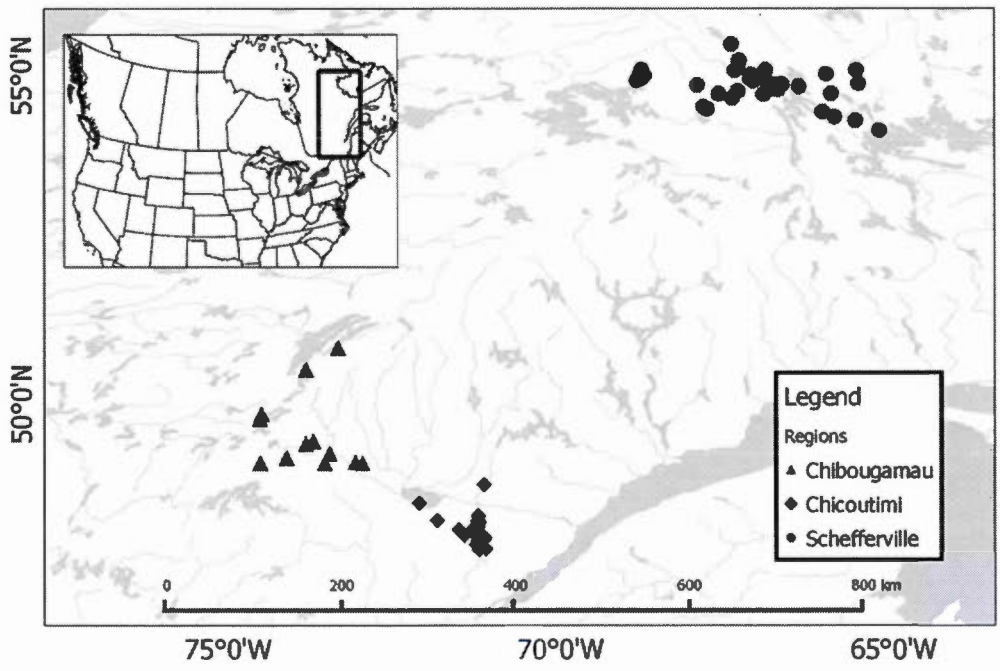

Figure 2.3 Map of the study area. Lakes are indicated with the symbols associated with each of the three boreal regions (Chicoutimi, Chibougamau and Schefferville) of Québec, Canada.

Tableau 2.3 SEM direct and indirect standardized effects for explaining ZP using environmental factors; chlorophyll a (chl*a*), percent wetland cover in the catchment (%WET), lake area (LA), water temperature (Temp), total phosphorus (TP), percent forest cover in the catchment (%FOR) and the predation index (pred). In general, the total direct effect of environmental factors on ZP is more important than their indirect effect.

	Direct		Indirect	
	+	-	+	-
Size	0.35			
Biom		-0.24		
Cumulative effect size	0.35	-0.24		
chl*a*	0.34			
Temp	0.24		0.10	-0.06
DOC			0.18	
TP			0.10	
Cumulative effect size	0.58		0.38	-0.26
LA		-0.32		
% WET		-0.27	0.04	
% FOR			0.13	-0.08
Cumulative effect size		-0.60	0.40	-0.10

2.7.1 Zooplankton biomass and body mass estimation

To estimate zooplankton biomass, preserved samples were split using a Folsom plankton splitter, and total biomass, as well as size of each zooplankter (equivalent spherical diameter ; ESD) was measured using a Laser Optical Plankton Counter equipped with a lab circulator (LOPC ; Rolls Royce, Canada), following methods outlined in Finlay et al. Finlay *et al.* (2007). All particle-specific ESD values for each 15 µm bin were converted to biovolume (V) for ellipsoids, according to Sprules et al. (1998) as :

$$V = \frac{\Pi}{6}\left(\frac{ESD^3}{f^2}\right) \tag{2.1}$$

where, f is the ratio of individual length to width with an f-value of 1.72 established by Finlay *et al.* (2007) for Québec lakes. A specific gravity of 1 was assumed for conversion of V to wet mass (Peters and Downing 1984). Dry mass was calculated as 0.2 wet mass and carbon as 40% of dry mass (Peters et Downing, 1984).

2.7.2 Zooplankton production : Sample collection, processing, and incubations

All chitobiase-based productivity measurements used water collected with a peristaltic pump from a depth of 2 m, or 1m above the sediments for lakes shallower than 2 m. Pumped water was immediately passed through a 45 µm mesh and into 2 acid-washed, wide-mouthed, Nalgene bottles (500 mL capacity). The mesh was used to exclude any crustacean zooplankton from the incubation bottles, which were filled to the shoulder. Approximately 20 mL of water was sub-sampled from each replicate incubation bottle with a sterile syringe and passed through a non-protein binding 0.22 µm syringe-filter (Sarstedt) into an acid-washed scintillation vial. The mouth of each scintillation vial was covered with Parafilm, then capped,

and labeled. Each incubation bottle was again sub-sampled with this procedure every 6 hours for up to 36 hours (i.e. Times 6, 12, 18, 24, 30 and 36). The first sub-sampling (time 0) took place immediately following the initial filling of incubation bottles at the sampled lake. Following water collection, incubation bottles were kept in a refrigerated water bath. Multiple lakes were sampled each day and the water bath temperature was set to the mean sampling temperature at 0.5 m depth across the lake set. Time-specific sub-samples were refrigerated (4 °C) and enzymatic analysis was done within 7 days of sample collection. Sub-samples were kept on ice during transport to the lab.

2.7.3 Chitobiase preservation experiment

We ran a controlled experiment to determine the impact of (1) the preservation method and (2) the delay between sample collection and the enzymatic assay on enzymatic activity and consequently on production estimates. Preservation in the freezer almost completely denatured chitobiase activity (Figure 2.4) while preservation in the fridge or at room temperature, lead to differences between the chitobiase activity of a sample and chitobiase activity at t0 which only significant 20 days after sample collection.

2.7.4 Zooplankton production rates : Chitobiase assay

Refrigerated samples were kept in the dark at room temperature for 18 hours prior to chitobiase activity measurements. All enzyme assays were run in 4 mL capacity clear methylacrylate cuvettes. Assays specific to each incubation time-point were run in triplicate. Each reaction was initiated with the addition of 0.5 mL of the substrate, 4-methylumbelliferl-N-acetyl-n-D-glucosaminide (0.1mmol MBF-NAG ; Sigma) to 2 mL of sub-sample water and 1 mL of 0.15 M citrate-phosphate buffer (CPB ; pH 6.0 ; McIlvaine, 1921). Reactions were allowed to proceed at 25 °C for

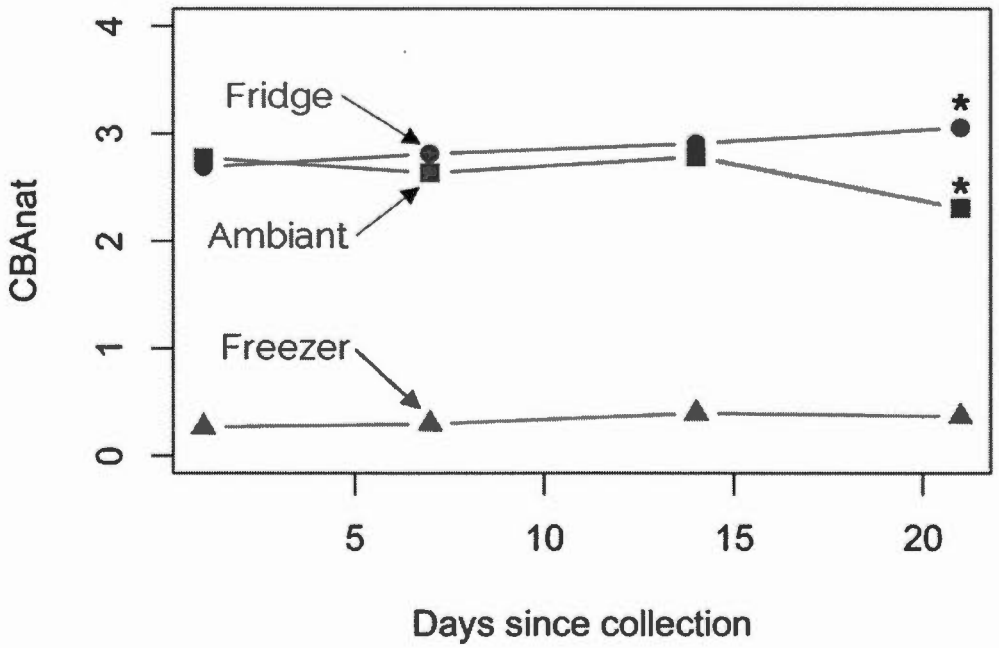

Figure 2.4 Comparison of ZPar predicted using the PD model and our ZPar estimates using the enzymatic technique.

60 minutes and were terminated with the addition of up to 0.5 mL 0.25 N NaOH (Sastri *et al.*, 2013). Chitobiase catalyzes the hydrolysis of MBF-NAG and the fluorescence of the liberated MBF moiety was measured at 360 nm excitation and 450 nm emission wavelengths using either a Cary Eclipse Fluorescence Spectrophotometer (Varian, USA) in 2011 or a Shimadzu RF-5301PC (Shimadzu, Japan) in 2012. Background fluorescence was measured in reactions for which the addition of NaOH preceded the addition of MBF-NAG. Fluorescence for each lake-specific set of assays was converted to nmol MBF using a 0-25 nmol dilution series of MBF (Sigma).

2.7.5 Calculation of zooplankton production (ZP) rates

A detailed description of calculations is presented in Sastri *et al.* (2013). In summary, biomass production rates (ZP) were calculated as :

$$ZP = \Delta B / T_{CBA} \tag{2.2}$$

where, ΔB represents the sum of biomass produced between molts (via somatic growth) for all members of the actively molting crustacean zooplankton community. This value was calculated by applying the measured CBA_{NAT} (i.e., CBA at time 0) to the relationship between the change in individual body mass (ΔB) and chitobiase activity for freshwater zooplankton that was previously developed by Sastri et al. 2013 for freshwater zooplankton : $log_{10}\Delta B$ = -2.076 + 0.685 • $log_{10}CBA_{NAT}$ (3). In equation (2), T_{CBA} is the total time taken for all developing animals in the community to produce ΔB (between molts). T_{CBA} was calculated from the regression of incubation time against CBA measured at each time-step. Thus, T_{CBA} is equivalent to the time required for CBA in the incubation bottle to reach 0 mmol MBF L-1 hr-1 ; and was calculated by setting CBA (y-value) to

0 in the regression of time against CBA at each incubation time-step. Sastri et al. (Sastri et al. 2013, 2014) and earlier field studies employing the chitobiase method (see Sastri *et al.*, 2012) found that exponential decay models best fit their decay rate measurements. These studies all measured chitobiase activity in samples within several hours of the conclusion of incubations. For this current field study, however, samples were kept in the refrigerator for up to 7 days before assays, and we found a better fit with a linear decay versus an exponential decay model. Some decay rates were characterized by relatively high scatter and replicates with R^2 values < 0.40 were excluded. Further, time-point-specific CBA outliers were identified as having a residual greater than 3 according to a studentized residual analysis. All decay rates (% $hour^{-1}$) were corrected for differences between sampling temperature and incubation temperature using a Q_{10} of 3.15 (Sastri *et al.*, 2009).

2.7.6 Comparison between our ZP estimates and the PD model

We applied the PD model to our data to compare the predictions of the PD model to our ZP observations. To do so, we calculated maximum individual mass (Wm, the mass of the largest individuals in the community) for all our lakes. We then applied the PD model to our data using areal total zooplankton biomass (Biomareal), maximum size (Wm) and epilimnetic temperature (Temp). Finally, to compare to our daily estimates we divided the annual estimates from above equation by 200 (estimated length of the growing season in days) and by lake depth to obtain volumetric estimates. as in PD to build the following model (R^2_{adj}=0.60, p«0.001) :

$$ZP_{vol} = \frac{0.13 + 0.46log_{10}(Biom_{ar}) - 0.45log_{10}(W_m) + 0.04Temp}{lake\,depth} \tag{2.3}$$

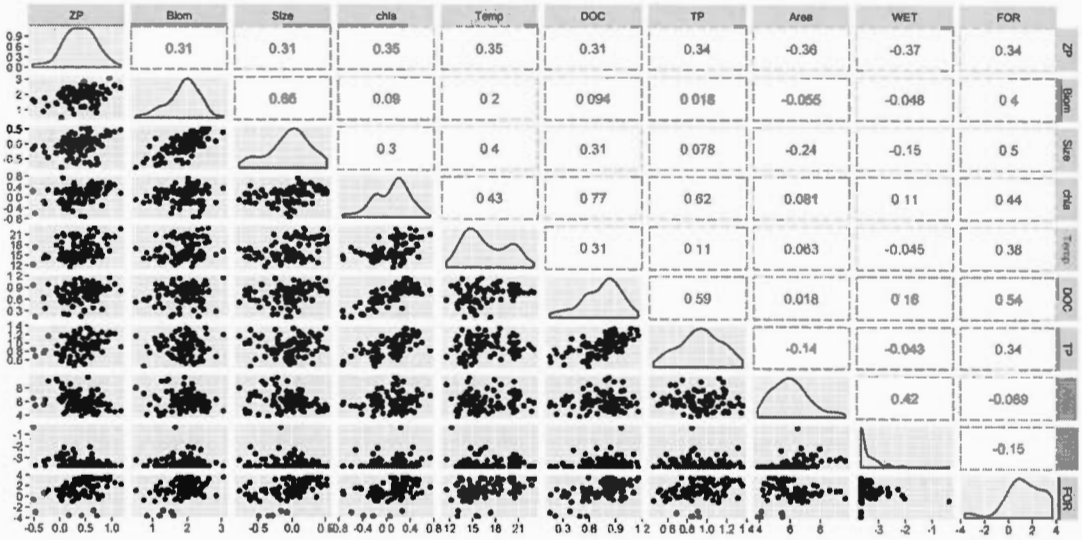

Figure 2.5 A matrix of plots with biplots below the diagonal, density distribution on the diagonal and correlation coefficients above the diagonal for each variable included in the final SEM. This plot was created using the ggpairs function from the GGally R package (Schloerke et al. 2014) using the transformed variables

To compare the estimates from the PD model and our estimates we computed the Mean Absolute Error (MAE).

Tableau 2.4 The standardized and unstandardized coefficients and associated P-values for each link in the final SEM (Figure 1b). Causal links are represented by a single ~ and correlations by a ~~.

Link	Coefficient	Standardized coefficient	P-value
ZP ~Biom	0.25	0.35	0.00
ZP ~Size	-0.25	-0.24	0.02
ZP ~chla	0.38	0.34	0.00
ZP ~Temp	0.03	0.24	0.01
ZP ~Area	-0.09	-0.33	0.00
ZP ~%WET	-0.18	-0.27	0.00
Biom~%FOR	0.11	0.40	0.00
Size ~Temp	0.02	0.24	0.00
Size ~Area	-0.05	-0.21	0.00
Size ~%FOR	0.06	0.40	0.00
chla~DOC	0.70	0.54	0.00
chla~TP	0.39	0.29	0.00
chla~temp	0.02	0.23	0.00
DOC ~%WET	0.11	0.25	0.00
DOC ~%FOR	0.08	0.58	0.00
TP ~%FOR	0.04	0.34	0.00
Biom~~Size	0.07	0.62	0.00
DOC ~~TP	0.02	0.54	0.00

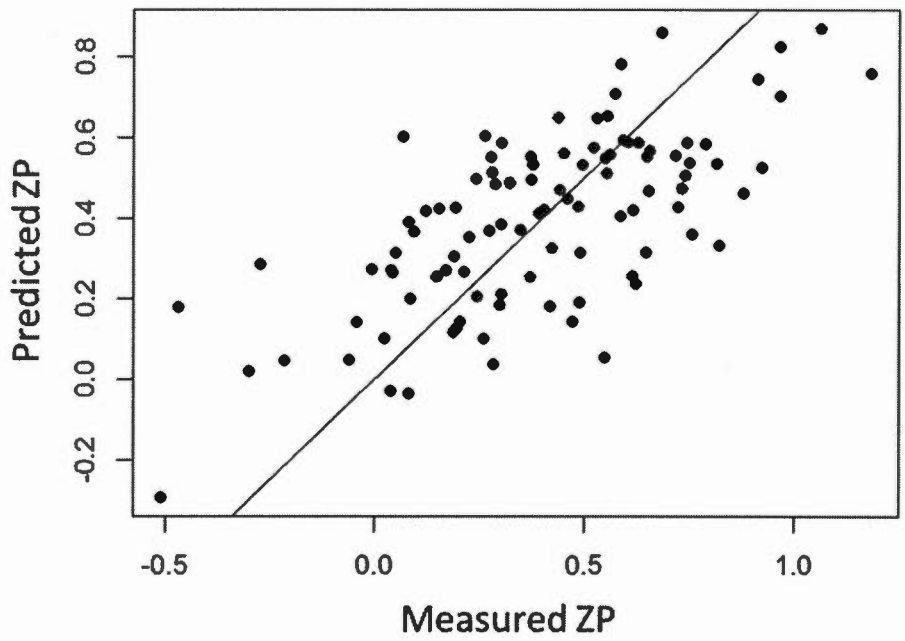

Figure 2.6 The predicted ZP in the best regression model (table 2, model I) versus measured ZP. The 1 :1 line is shown on the diagonal.

CHAPITRE III

FUNCTIONAL COMMUNITY STRUCTURE MODULATES ZOOPLANKTON PRODUCTION ACROSS BOREAL LAKES

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N.B. References cited in this chapter are presented at the end of the thesis

3.1 Abstract

Although there is a general consensus in ecology that diversified ecosystems tend to be more productive, it is still unclear whether aquatic ecosystems follow this general trend. Moreover, current evidence is primarily based on the results of experimental studies in which biodiversity was assesed through species richness. Consequently, we still have a poor understanding of how community performance may be linked to the various features of community structure in aquatic ecosystems. Here we present a study that explicitly assesses the effect of both taxonomic and functional diversity on crustacean zooplankton production across boreal lakes spanning wide limnological ranges. After controlling for the effect of environmental factors on biomass production, we found that zooplankton productivity was linked to the dominance of certain filtration strategies (*Daphnia*-filtration and *Chydorus*-filtration). Furthermore, communities with a clear dominance of key functional types, and therefore more functionally uneven, tended to also be more productive, an identity effect that was captured by functional evenness. Not only did both the functional diversity and composition of zooplankton communities affect crustacean zooplankton productivity in boreal lakes, but the magnitude of the compositional effect was comparable to the aggregated effect of environmental variables. Overall, our study demonstrates that across boreal lakes, community structure plays an important role in the regulation of zooplankton biomass production, a pivotal function at the ecosystem level. Contrary to the general ecological literature, however, the relationship between functional diversity and productivity was negative, which could be explained by an identity effect.

3.2 Introduction

A major objective of community ecology is to understand not only what factors influence biotic diversity, but also how the alteration of biotic diversity (in terms of genes, functional types or taxonomy) influences the functioning of ecosystems(see Hooper *et al.*, 2005; Gamfeldt et Hillebrand, 2008). The rapid expansion of research on biodiversity effects on ecosystem functioning (BEF) has been triggered by evidence of the massive impact of human activities on biodiversity and as a consequence the feedback on the functioning of natural ecosystems and the services they provide (Cardinale *et al.*, 2012). Early BEF studies were conducted mainly in an experimental context, which was a fundamental step to develop clear ecological mechanisms driving BEF and their consistency across ecosystems. From this body of work, it was concluded that "There is now unequivocal evidence that biodiversity loss reduces the efficiency by which ecological communities [...] produce biomass" and that a "biodiversity effect seems to be remarkably consistent [...] across trophic levels" (Cardinale *et al.*, 2012). However, a careful look at both observational and experimental studies (Figure 3.1) demonstrates that the applicability of such a conclusion to aquatic ecosystems is not supported. In aquatic ecosystems, an equivalent number of studies (7) have reported both positive and negative effects of species richness on biomass production or standing biomass, while for evenness, all studies to date have reported either no relationship or a negative one (Figure 3.1). Furthermore, because of the relative simplicity of early BEF experiments (very small temporal and spatial scales with unrealistically low richness levels), more recent studies have begun to test these relationships under more complex experimental scenarios and in natural ecosystems, with expectations ranging from stronger effects because of larger scales (Cardinale, 2011) to reduced effects because of greater environment filtering in natural ecosystems (Grace *et al.*, 2007) .Further studies of ambient communities in complex natural ecosys-

tems can resolve these contrasting expectations, and improve our understanding of how the relationship between community structure and productivity is shaped in nature (Grace *et al.*, 2007). Understanding the relative importance of community structure is especially critical in aquatic ecosystems, for which experimental results often run counter to the more abundant terrestrial literature (Figure 3.1). In addition, because BEF deals with the functional role of taxa in ecosystems, a strictly taxonomic conception of biodiversity (usually richness) is limited and generally uninformative with respect to mechanisms underlying biodiversity effects (Díaz et Cabido, 2001; Hooper *et al.*, 2005; Cadotte *et al.*, 2011). Indeed, in the rare cases when they have been compared, functional diversity effects on ecosystem functions (EF) have been stronger than those of taxonomic diversity (Díaz et Cabido, 2001; Mokany *et al.*, 2008).

Biomass production has been widely studied as a key EF (Vogt *et al.*, 2010; Messmer *et al.*, 2014; Weis, 2016), as it plays a crucial role in the regulation of material and energy flows through biotic communities (Cyr et Pace, 1993; Hébert *et al.*, 2016). Many different mechanisms have been invoked to explain how the structure of biotic communities, taxonomic or functional, affect their biomass production (see Cardinale *et al.*, 2009).Generally, mechanisms can be grouped into two major, but not mutually exclusive, hypotheses : the diversity and the mass-ratio hypothesis. The diversity hypothesis, favoured in early BEF studies, postulates greater production by more diverse communities because of complementarity between taxa or functional types (i.e. greater niche partitioning and facilitation, Tilman, 1999). On the other hand, the mass-ratio hypothesis postulates that it is mainly the functional traits of the dominant species that matter, and consequently we expect that ecosystems in which more efficient species are selected and become dominant, biotic communities will be more productive in average (selection effect, Aarssen, 1997; Huston, 1997).

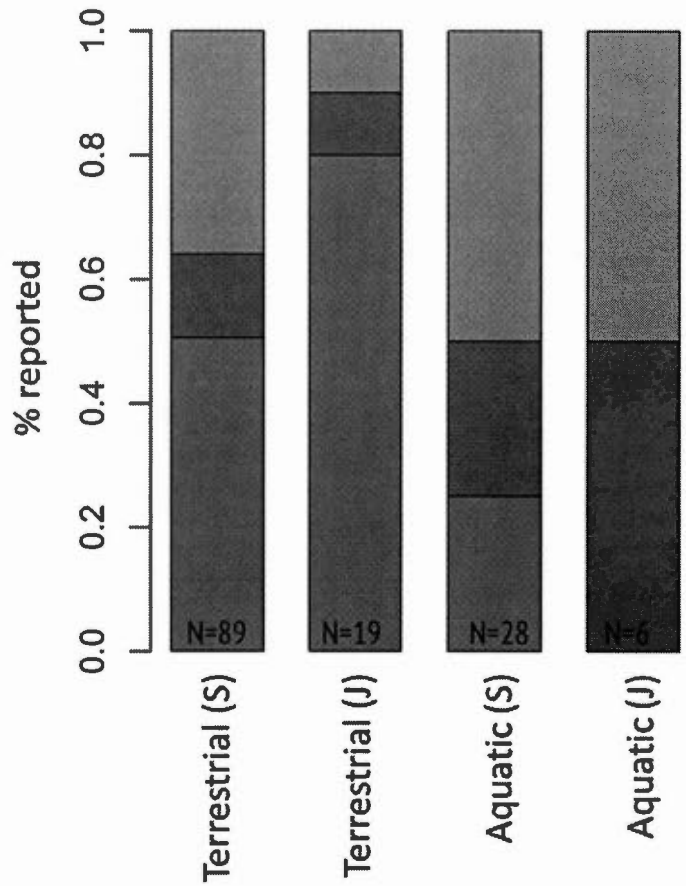

Figure 3.1 Summary of the reported relationships (positive in green, negative in red and no relationship in grey) between standing biomass or biomass production and diversity (richness, S and evenness, J) in terrestrial and aquatic ecosystems by observational and experimental studies (mainly). For each bar, the total number of studies (N) is reported. Data from Balvanera et al. 2006 and Rohr et al. 2016.

In aquatic ecosystems, zooplankton represent the key trophic link between energy mobilizers (i.e. phytoplankton and bacteria) and macroinvertebrates and fish, thus playing a critical functional role. The way in which secondary (zooplankton) production responds to shifts in zooplankton community structure and composition therefore has the potential to greatly influence the fluxes of energy and matter at the whole ecosystem scale in lakes and oceans. While several experimental studies have reported that zooplankton standing biomass is negatively related to community richness (Norberg, 2000; Downing et Leibold, 2002; Jonsson et Malmqvist, 2003; Steiner *et al.*, 2005), to our knowledge no studies to date have assessed if this relationship extends to zooplankton production rate as a function of the functional diversity and composition of zooplankton communities.

Here we explicitly address these gaps, and examine the potential role of the functional structure of community in modulating crustacean zooplankton community production rates across a wide range of boreal Lakes. To isolate the potential influence of community structure on zooplankton production (Figure 3.2, path 1) we accounted for the effect of standing biomass as well as of a suite of environmental factors (Figure 3.2, path 2). To further explore the effect of community structure, we examined the relative influence of functional diversity acting through complementarity (FD in Figure 3.2) versus that of functional identity (FI in Figure 3.2), acting through species selection. This is the first BEF study on crustacean zooplankton to include a direct measure of community performance (zooplankton production rate, ZP), as opposed to the widespread use of static indices, such as standing stock of biomass, as a dimension of ecosystem function (see Chapter II). Having a functional endpoint that addresses community production and turnover is particularly relevant for the study of planktonic communities, where biomass is regulated by multiple bottom up and top down factors and which often is not a good proxy of performance.

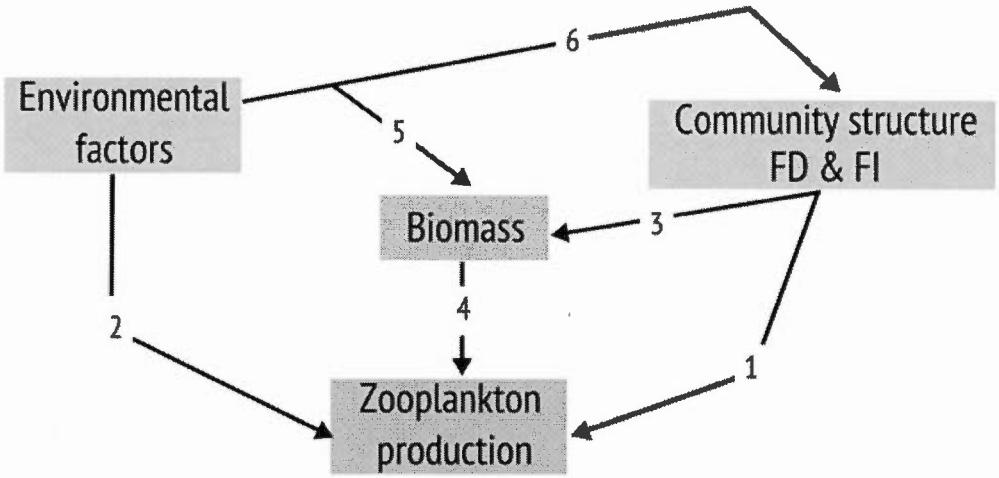

Figure 3.2 Conceptual causal diagram of the relationship between zooplankton production and community structure; functional diversity (FD) and functional identity (FI). Based on the second chapter. Paths are represented by numbers.

3.3 Materials and methods

Over the course of two summers (2011, 2012), we sampled zooplankton community structure, crustacean community production (ZP) and a wide range of limnological variables in 84 lakes from two environmentally and geologically distinct boreal regions across Quebec, Canada (Table 3.1, Figure 3.3); 17 lakes were sampled more than one time, leading to 106 samples. The temporal separation between samples (38-74 days) was enough to assume independence for both environmental conditions and communities. All lakes were accessed either by the road or using a floatplane and were sampled at the deepest point.

3.3.1 Environmental variables

To characterize the environment, we measured several lake and catchment level, variables. We measured mean epilimnetic temperature, chlorophyll (*Chla*), total

Tableau 3.1 List of variables included in the final SEM model

Variable (abbreviation)	Units	Mean	Range	Transformation
Zooplankton biomass production rate (*ZP*)	$mgC/m^3/day$	3.21	0.31-15.3	log_{10}
Water temperature (*Temp*)	°C	16.9	11.6-23.0	
Chlorophyll*a* (*chla*)	µg/L	1.5	0.2-5.5	log_{10}
Lake Area (*Area*)	m^2	$9.4x10^7$	$7x10^3 - 4x10^9$	log_{10}
Zooplankton biomass (*Biom*)	µgC/L	289	0.02-6978	log_{10}
% wetland cover in catchment (*WET*)	%	1.3	0-41	Loggit
% forest cover in catchment (*FOR*)	%	75.1	0-100	Loggit
Functional evenness (*FEve*)		0.46	0-0.97	
% *Chydorus*-filtration (*C-filtration*)	%	0.2	0-16	Loggit
% *Daphnia*-filtration (*D-filtration*)	%	20	0-74	Loggit

phosphorus (*TP*), dissolved organic carbon (*DOC*). Vertical water temperature (°C) profiles were taken using a multi-parameter sonde (YSI, Yellow Springs Instruments, OH, USA). Water samples for phytoplankton biomass (*Chla*; µg L^{-1}), TP (µg L^{-1}), and DOC (mg L^{-1}) were collected from 0.5 m depth in all lakes using a Van Dorn bottle. In the lab *Chla* was extracted with 90% hot ethanol and absorption was measured spectrophotometrically before and after acidification to account for phaeophytin (after Nush, 1980; Lorenzen, 1967); TP was measured from water samples using the molybdenum-blue method following persulfate digestion (Cattaneo et Prairie, 1995); and DOC concentration was measured on an O.I. Analytical (Texas, USA) TIC/TOC using 0.45m filtered water after sodium persulfate digestion. We also determined lake and watershed areas using the ArcGIS V10 from the National Topographic Data Base (NTDB), and for each catchment we estimated forest and wetland cover (%) obtained from (Geobase, 2009).

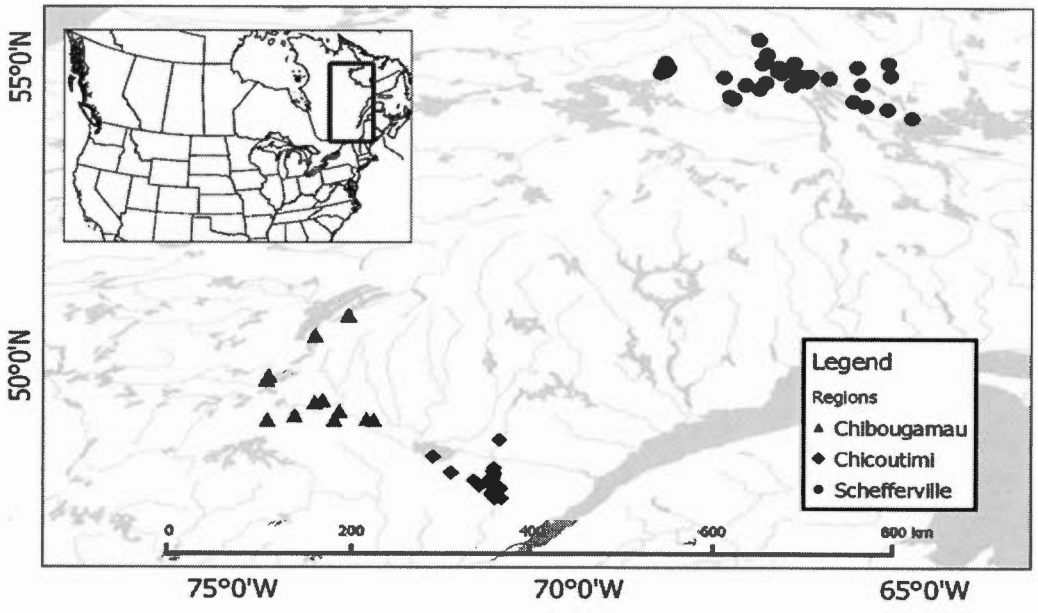

Figure 3.3 Map of the study area. Lakes are indicated with the symbols associated with each of the three boreal regions (Chicoutimi, Chibougamau and Schefferville) of Québec, Canada.

3.3.2 Zooplankton community structure

Zooplankton communities were sampled using a 110 µm mesh, 0.30 m mouth diameter conical plankton net, equipped with a flow meter (General Oceanics, USA), hauled vertically from 1 m above the lake bottom to the surface. Net contents were anaesthetized in carbonated soda water and then preserved in 75% ethanol (final concentration). Crustacean zooplankton were identified at the species level when possible, using an inverted microscope (50-400X) and individuals were counted until a total of 200 individuals had been enumerated. For each taxon present in a lake, the length of 20 mature individuals was measured and biomass by taxon was estimated using length-dry-mass regressions (McCauley, 1984; Culver *et al.*, 1985).

The objective of the study was to understand the link between zooplankton community structure (composition and diversity) and production in boreal lakes. We thus selected functional traits directly related to zooplankton bottom-up and top-down trophic interactions in lakes. The selected traits reflect how zooplankton organisms interact with their environment (response or effect traits, see Hooper *et al.*, 2005),as they have the potential to influence the flux and energy and matters in lakes at the ecosystem level. Crustacean zooplankton functional trait values were obtained from the literature (see Barnett *et al.*, 2007) and included (i) feeding type and (ii) trophic group. We also used the average individual size of each taxon, from our measurements, as an integrative functional trait of body size (Brown *et al.*, 2004; Litchman *et al.*, 2013; Hébert *et al.*, 2016) related both to resources acquisition and predation avoidance (Table 3.2). For functional identity, we only used the feeding strategy as functional trait, because of the important overlap with the trophic position trait. For functional diversity, we selected indices to capture the richness and evenness components of diversity. We used Villéger's

functional diversity indices (Villéger *et al.*, 2008) : functional richness (FRic), functional evenness (FEve), as well as functional dispersion.Functional diversity indices were measured using a multidimensional space, in which each axis represents a functional trait. Functional richness measures how much of the functional niche space is occupied (Schleuter *et al.*, 2010), and is measured as the volume of the functional space (using a convex hull fit). Thus, when there are important functional differences between species in a sample, the functional space and the convex hull volume will be large. Functional evenness (FEve) measures the regularity of the distance between species in trait space (Schleuter *et al.*, 2010). Finally, functional dispersion (FDis) is the mean of the distance of each species to the centroid of all species within functional trait space. FDis is higher when many species are far from their centroid. Functional diversity indices cannot be calculated with <3 species, thus in such samples functional diversity values were set to zero. All functional diversity indices were estimated using the *dbFD* function (FD R library, Laliberté *et al.*, 2014).

3.3.3 Zooplankton Production rates

Community-level biomass production rates by crustacean zooplankton were estimated using a recently developed enzymatic method (Sastri *et al.*, 2009,0). The method is based on the ambient activity of the chitobiase enzyme (CBA), which is produced by crustacean zooplankton during moulting. To estimate CBA production rates, we measured the decay rate of the enzyme in a filtered water sample during dark incubations. Assuming that the amount of CBA in the water column is roughly at steady state within the time frame of the incubation, the production rate in the water column should thus be equivalent to its degradation rate in an in vitro incubation that contains no zooplankton (Sastri *et al.*, 2009).This method is especially appealing because it integrates *in situ* biomass production rates of the entire crustacean community, and unlike many previous methods, it

can measure production rates (ZBP) on a time-scale (daily) that is more relevant to zooplankton community turnover rates. Finally, it is also less labour intensive, which enables broad-scale sampling and comparative analyses, like the one we present here. For mode details on the measurement of zooplankton production rates see Sastri et al. (2013).

3.3.4 Statistical analyses

We used redundancy analysis (RDA see Legendre et Legendre, 1998) to visualize the potential relationships between the different feeding strategies (functional traits) and diversity indices with environmental factors, using the rda function in the *vegan* R library (Oksanen *et al.*, 2015). Prior to the RDA we did a forward selection of environmental variables based on AIC using the ordistep R function (also within the vegan library), consequently only environmental variables significantly linked to community structure and diversity were used in the RDAs. Furthermore, to visualize the relationship between zooplankton feeding strategies, diversity indices and zooplankton production within a lake, we passively projected ZP using the *envfit* function (vegan R library, Oksanen *et al.*, 2015) on the community and diversity RDAs.

To more formally investigate the relationship between crustacean zooplankton biomass production rates (ZP), community structure (diversity and functional composition), while controlling for standing biomass and environmental factors, we used structural equation modelling (SEM Bollen, 1989; Shipley, 2002; Grace, 2006). Because in SEM the coefficients of each variable are evaluated while holding all other variables constant, when zooplankton biomass is included in the model, we assume that every direct link to ZP represents a link to zooplankton-specific production (hereafter termed productivity), which is a measure of the turnover of community biomass. As our starting point, we constructed a SEM model, using

Tableau 3.2 Zooplankton functional traits used in this study.

Traits	Values
Feeding type	*Bosmina*-filtration
	Chydorus-filtration
	Daphnia-filtration
	Sida-filtration
	Stationary Suspension
	Raptorial
Trophic position	Carnivore
	Omnivore-Carnivore
	Omnivore
	Omnivore-Herbivore
	Herbivore
	Immature
Size	Mean size

Lavaan R library (Rosseel, 2012), that included all the environmental factors selected in the final SEM model of Chapter II with standing biomass and community structure variables (diversity indices and feeding types, see Table 3.2 and Figure 3.1a). We also added indirect links from environmental factors on community structure and standing biomass. Subsequent model specifications sought to iteratively improve the explanatory power of the SEM by including or removing direct interactions based on p-values (highest p-value interactions removed at each iteration). Because our selection procedure removed variables, our models are not nested and we thus relied on the R^2 for the relationship between standing biomass and ZP to identify improved model specifications (although overall model AICs are also presented). Additionally, we used modification indices to assess whether any particular relationship could improve model AIC by more than 5. SEM overall significance was tested using the textitp-value of the goodness-of-fit criteria (χ^2). Finally, variables with no direct or indirect path to biomass or ZP were removed from the final SEM.

3.4 Results

The RDAs provided general insight into the existing relationships between the various community response variables, environmental variables and zooplankton production (ZP). In the RDA based on the functional traits (Figure 3.4a), we observed that most lakes were either dominated by stationary suspension or D-filtration (*Daphnia*) and raptorial feeding strategies. Furthermore, the latter were favoured in warmer lakes (Temp) with a more forested catchment (%FOR) while all the other feeding strategies were favoured in smaller lakes (LA). Finally, ZP was positively associated with the second RDA axis, and was consequently higher in lakes where D-filtration and raptorial feeding were the dominant feeding strategies.

The first axis of the diversity RDA (Figure 3.4b) was clearly a diversity axis, as all diversity indices loaded positively. On the second RDA axis, functional richness (FRic) loaded positively and functional evenness (FEve) negatively. In general, all the functional diversity indices were higher in lakes located in a catchment with a higher proportion of forest (%FOR) and wetlands (%WET) while functional richness was also higher in lakes with more chl*a*. ZP was negatively associated with the diversity axis.

The fit of our initial SEM (including all the diversity indices and feeding strategies) to the data was poor (χ^2=107.5, d.f. = 36, model p = 0.0001) as a result of many non-significant paths. Sequentially removing these nonsignificant paths revealed three significant links between community structure and ZP : functional evenness (FEve), the proportion of D-filtration (%DF) and C-filtration (%CF). In the final model, FEve could not be replaced by any other diversity index, even taxonomic evenness. In the case of feeding strategies, %CF could be replaced by %BF (*Bosmina*-filtration), but the relative important of B-filtration was lower than %CF. Our final model (χ^2=23.6, d.f. = 17, model p = 0.13, Figure 3.5)

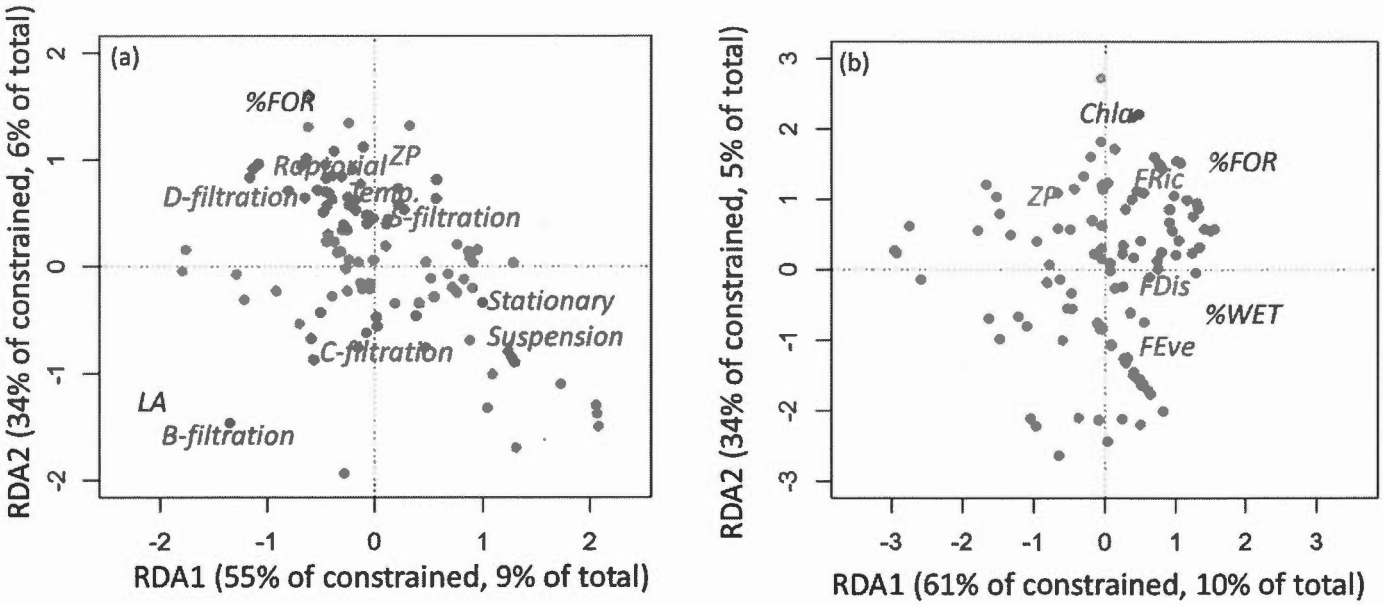

Figure 3.4 RDA of functional traits (a) and functional diversity indices (b) constrained by environmental factors. Only environment factors with significant associations with the PCA axes are displayed. Functional traits are displayed in green, environmental factors in red, biomass in blue and ZP in orange. Where LA, lake area; %FOR, % forest in the catchment; Temp., epilimnetic temperature; chl*a*, chlorophyll a concentration; %WET, % wetland in the catchment; Biom, zooplankton standing biomass; ZP; zooplankton production; FRic, functional richness; FEve, functional evenness; FRic, functional richness.

explained 46% of the variation in ZP, 8% of the variation in zooplankton standing biomass (Biom), 7% of FEve and 17% of %DF. While no environmental variables could explain the %CF in a lake, the proportion of D-filtration (%DF) was positively related to the proportion of forest in the catchment (%FOR) and lake area (LA), and FEve was positively related to the proportion of wetlands in the catchment (%WET). Finally, direct environmental predictors of ZP in our model (Temp, chl*a*, LA and %WET), were the same as those selected in the model in Chapter II, with the exception of mean size (not included in the current model). The cumulative positive effect of community structure variables was 0.40 and the negative effect was -0.31. The cumulative positive direct effect of environmental factors was 0.32 and the negative effect was 0.44, while the indirect positive effect, through community structure, was 0.15 and the negative indirect effect 0.03.

3.5 Discussion

In a previous chapter (Chapter II) we had shown that the variability in zooplankton community production across boreal lakes could be directly explained in part by a core set of environmental factors, which included phytoplankton biomass (*chla*), lake area, temperature and wetland cover. Here we show that all the environmental variables directly explaining ZP in the SEM (direct links, figure 3.5) were also selected in the RDA to explain functional composition and diversity across sites (Figure 3.4), suggesting that in boreal lakes there is a strong coupling between environmental drivers, community structure and zooplankton production. In this regard, our results clearly show that zooplankton production (ZP) is regulated by both environmental factors and zooplankton community structure, and structural equation modelling was useful in understanding the nature of the links that exist between these two sets of drivers and their complex interactions. The cumulative effect of factors associated with community structure attributes(both functional and taxonomic) on zooplankton production (ZP) in lakes was compa-

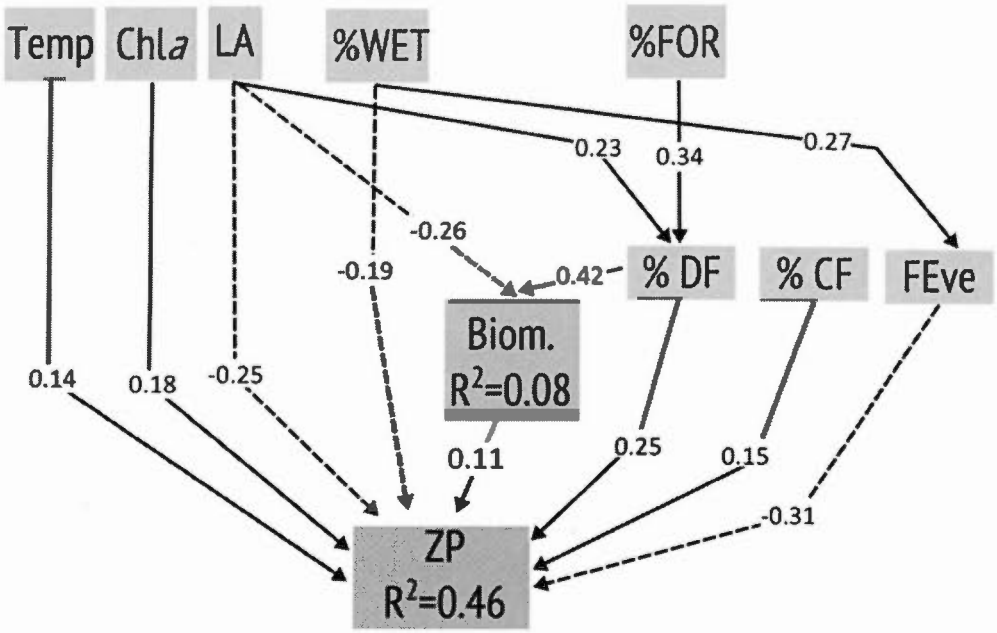

Figure 3.5 The final SEM, to explain zooplankton production (ZP) using environmental variables (in red), zooplankton standing biomass (Biom, in blue) and zooplankton community structure (in green). Standardized coefficients are displayed on each line. The community structure metrics selected in the final model were functional evenness (FEve), and the *Daphnia*-filtration (%DF) and *Chydorus-filtration* (%CF) functional types was. Where LA, lake area; %FOR, % forest in the catchment; Temp, epiliinnetic temperature; chl*a*, chlorophyll a concentration; %WET, % wetland in the catchments.

rable to that of environmental factors, even after considering the indirect influence of environmental factors on community structure. In spite of the inherent environment complexity in these lakes, and the large environmental gradients that exist among them, we observed a strong link between biomass production and the structure of communities,particularly at the functional level.

The dominant zooplankton feeding strategies across all lakes were D-filtration and stationary suspension (Figure 3.4a). Based on the ordination, ZP was on average higher in lakes with a higher proportion of D-filtration, which was also confirmed in the SEM. D-filtration is known to be an efficient feeding strategy in oligo- to mesotrophic lakes with high food quality (McNaught, 1975; Richman et Dodson, 1983; Barnett *et al.*, 2007), leading to greater competitive capacity, mainly in the pelagic zone of lakes where small edible phytoplankton are abundant. Interestingly, our SEM also showed that zooplankton communities with a higher proportion of C-filtration were also more productive. C-filtration is a completely different feeding strategy from the pelagic D-filtration,which involves using an alternative resource by scraping periphyton from hard surfaces (Barnett *et al.*, 2007). Thus, C-filtration is favoured in the littoral zone of macrophyte-dominated lakes, where substrates and light enable abundant periphyton growth. Unfortunately, we do not have any direct measurements of the proportion of macrophytes in our study lakes. Furthermore, not all shallow lakes have macrophyte beds, and this may explain why we did not find relationship between C-filtration and any environmental factors. In sum, these results on functional feeding types indicate that both C and D-filtration feeding strategies can be highly efficient and that dominance of these functional traits results in higher overall ZP, once all other major regulating factors are accounted for.

The ordinations that we carried out further showed that ZP loaded negatively on the diversity axis (Figure 3.4b), in what appears to be a recurrent observation

in aquatic ecosystems (Figure 3.1). In our case, however, the only diversity index selected in the final SEM was functional evenness (FEve), which was in fact the strongest direct predictor of ZP. Furthermore, FEve could not be replaced by taxonomic evenness (Pielou's J), which supports the contention that the use of functional indicators provides more insight into the relationship between community structure and the performance of these communities, especially in the context where environmental factors also vary (i.e. in observational studies). Moreover, in contrast to the developing consensus that diversity enables productivity across all ecosystem types (see Cardinale *et al.*, 2012), our results clearly suggest that in lakes, dominance of specific functional types taxa (i.e. lower FEve or dominance by C-filtration or D-filtration) is associated to higher zooplankton productivity. Our results thus confirm that previous reports of a negative relationship between diversity and standing stock in lakes can be now extended to actual performance by these aquatic communities. Consequently, the identity of the dominant functional types is what is relevant for the production of biomass in zooplankton communities,which supports the mass-ration hypothesis. Even if functional evenness was the strongest individual predictor of ZP, the negative relationship between the two also supports the mass-ratio hypothesis (selection effect), as we found no support for any effect of complementary (the diversity hypothesis).

Theoretically, a negative relationship between biomass production and evenness, like the one we observed, is expected when the dominant species or functional type is in strong competition with the rest of the community (Rohr *et al.*, 2016), and this is, in essence, what we observed using functional evenness. As FEve is a biomass-weighted measure, a low functional evenness implies a large functional difference (and therefore low niche overlap) between the dominant functional type(s) and the rest of the community. Moreover, the dominant feeding strategy varied greatly between lakes (Figure 3.4a), indicating that different feeding strategies are

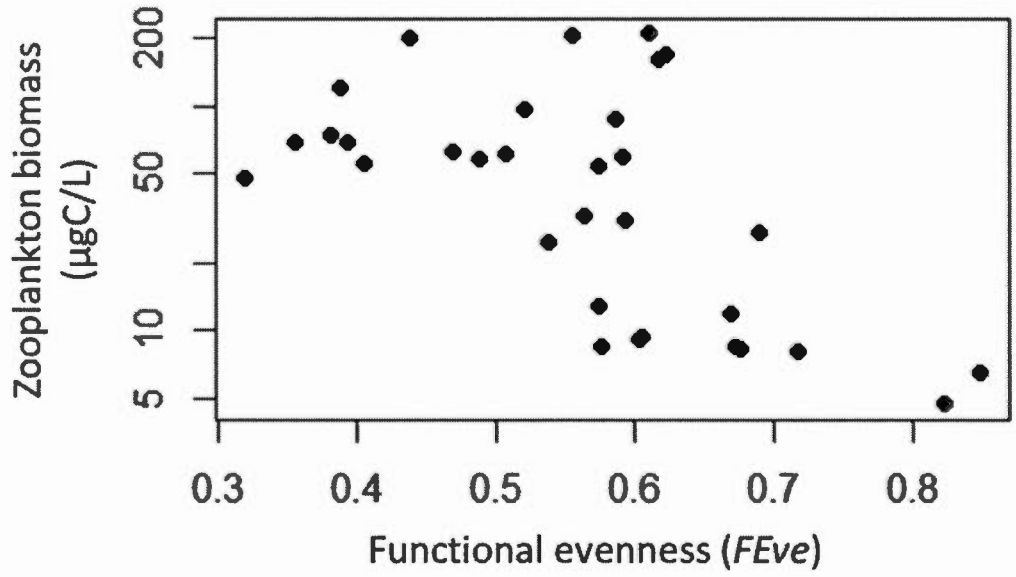

Figure 3.6 The relationship between functional evenness and zooplankton standing biomass in lake Croche.

favoured in different lakes. The temporally dynamic nature of boreal lakes may explain this pattern, as the sites were not all sampled at the same point in their seasonal succession. The dominant zooplankton feeding strategy will vary over the seasonal succession (Sommer *et al.*, 1986, 2012), driven by temporal variation in water temperature, competition, predation and resources (DeMott et Kerfoot, 1982; Gliwicz et Lampert, 1990). Variation in the successional point of each lake could thus affect the strategy that was dominant at our sampling time. Hence, the reason why functional evenness is such a strong predictor of ZP in boreal lakes could be that it effectively tracks internal dynamics within the zooplankton community, and how the community responds to maximize the utilization of available resources at different times of the seasonal cycle.

Zooplankton communities in boreal lakes undergo a complete succession cycle over

an annual cycle, and this is underlain by a very fast species and biomass turn over, and variation in FEve within lakes is in fact the result of the alternate of dominance by a specific functional type and periods of high functional evenness when diverse strategies are coexisting. If the patterns that we observe at the landscape level may reflect the mosaic of successional stages that occurs across lakes, we would thus expect functional evenness to be low at times of high biomass and production, and vice versa. To test this idea, we used seasonal time-series data from the well-studied Lac Croche (Sastri et al. 2013, Fig. 6), and found that the variation in the value of FEve ranged from 0.3 to 0.9 within the growing season, which resembles the range of variation observed in our study at the entire landscape scale (FEve = 0 to 0.97). Furthermore, we found that, as predicted, FEve within lake Croche varied inversely with biomass, with low FEve (dominance of a specific functional type) corresponded to high community biomass, and higher FEve observed during intervals between functional dominance peaks, when functional evenness was high community biomass was low.Which suggests that FEve on the landscape may reflect differences in successional stages that exists in lakes across the boreal biome. From a community perspective, performance at any environmental and resource scenario does not appear to be maximized via functional or taxonomic diversity, but rather by the selection of specific functional types that are able to best exploit the particular scenario. In this context, the extant taxonomic and functional diversity still plays a key role, but not in the performance itself, rather as a potential seed that feeds the functional succession that maximizes resource utilization.

The main goal of our study was to advance our understanding of BEF in aquatic ecosystems, and more specifically in natural lake zooplankton communities, and for this we incorporated several novel features including the use functional trait diversity and composition indicators, a more direct indicator of community pro-

duction rates representing EF, and a large-scale comparative approach across an extremely wide geographic and environmental gradient of boreal lakes. We have shown that to understand the regulation of zooplankton production in lakes we need to take into account not only the effect environmental drivers, such as lake morphometry, water chemistry and resources, but also aspects of community structure, which strongly modulate the environmental regulation. It is clear that there is a strong seasonal dimension to the spatial patterns that we have shown here, since these communities have such rapid community turnover that can influence the identity of traits relevant for EF, and also the degree to which communities are dominated by particular functions. Our results confirm that the regulation of community production, and especially the roles of community structure as well as the mechanisms explaining the relationship, are quite different between aquatic and terrestrial environments. This in turn suggests that a generalization regarding BEF across all types of ecosystems may not be possible, and it then becomes important to identify when and why these different ecosystems or communities diverge in their respective BEF, and whether these differences may be traced to aspects of energy flow, ecosystem size and dimensionality, as has been identified in the case of some other general ecological relations.

CHAPITRE IV

LIMITED FUNCTIONAL RESPONSES OF PLANKTON FOOD WEBS IN NORTHERN LAKES FOLLOWING DIAMOND MINING

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N.B. References cited in this chapter are presented at the end of the thesis

4.1 Abstract

There is a very limited understanding of the impact of diamond mining on the aquatic communities of downstream lakes that receive mine activity residues. For aquatic communities, assessing the response to mining, which can affect multiple variables concurrently, is not trivial, especially when a species-by-species approach is used. Thus, we assessed diamond mine impacts using changes in plankton functional composition enabling an integrated evaluation of the ecological responses of aquatic ecosystems. Over 19 years, we evaluated the functional responses of lake phytoplankton and zooplankton to water quality changes associated with mining activities in five downstream lakes of the Ekati diamond mine (NWT, Canada). Our results demonstrate that diamond mine activity shifted phytoplankton functional composition toward edible diatoms, and more recently the rotifer communities toward parallelepiped types, while for crustacean zooplankton we observed a reinforcement of the original functional composition. Following functional, rather than taxonomic changes enabled a more mechanistic understanding of the processes behind the impacts and should facilitate the generalization of impacts to other sites, permitting comparison of community shifts with other mining types.

4.2 Introduction

Mining activities in northern Canada have steadily increased over recent decades, and are expected to further grow by 91% between 2011 and 2020 (The Conference Board of Canada, 2013). Diamond mining has played an important role in recent expansion, with Canada becoming one of the main diamond producers in the world. Expansion is expected to continue as several new mining projects (e.g. Renard Project in Quebec, Jay Pipe at Ekati in the NWT) start operations within the next few years. As many different compounds are exported from a diamond mine to neighboring lakes (ERM, 2014), understanding the effects of such mining activities on water quality and consequently on surrounding ecosystems is crucial to minimize their impact, as well as to comply with federal, provincial and territorial laws on environmental protection.

In lakes, plankton are trophically important organisms as they largely control the flux of energy and matter in mostly unproductive northern ecosystems (Gu *et al.*, 1994; Kling *et al.*, 1992; Gu *et al.*, 1996). Consequently, mining effects on plankton should ultimately also have repercussions for the functioning of lake ecosystems, including higher trophic levels (e.g. fish). Moreover, as they have short generation times, plankton communities respond quickly to disturbances and are thus useful indicators to track environmental change, in addition to providing important insights on the general response of aquatic ecosystems (Whitton *et al.*, 1991; Carvalho *et al.*, 2013; Khalifa *et al.*, 2015).

The Ekati Diamond Mine is Canada's first diamond mine and has been in operation since 1998. This study was conducted in the Koala Watershed, one of the main watersheds influenced by the Ekati Diamond Mine. As a component of the Ekati Diamond Mine Aquatic Effects Monitoring Program (AEMP), phytoplankton and zooplankton communities in Koala Watershed lakes were sampled annually over

19 years, along with multiple water quality parameters and physical variables. We used these time-series to study how temporal changes in water quality impacted downstream plankton communities. We used a functional trait perspective for interpreting temporal community changes; specifically, we tracked changes in functional trait composition and size structure. Using a functional approach enabled us to establish a more general and mechanistic evaluation of the ecological response of lakes to mining activities with conclusions that could be more easily applied to other locations without reference to taxonomic detail. This approach is also likely to be more amenable to industry, requiring less taxonomic expertise if easily attributed traits provide the same information as more taxonomically-based approaches; saving time and money but still permitting valid environmental impact assessments. However, the correspondence of taxonomic and functional conclusions remains to be verified and was thus one of the goals of this study.

The main route by which diamond mining activities should affect aquatic organisms is through changes in water quality, via the regulated release of several concentrated compounds from a mine to the environment. Through such releases, increased concentrations of some trace elements (e.g. copper, aluminium) could have toxic effects on living organisms (AEMP appendix G, ERM, 2014). However, it was previously determined that in the Koala Watershed, no water quality parameters exceeded the lowest known chronic effect values for the most sensitive plankton species (AEMP appendix G, ERM, 2014). At the same time, the input of macronutrients (e.g. nitrogen, phosphorus) from watersheds is well known to influence the interaction of species within plankton food webs; affecting composition and diversity, with such effects being well established in the ecological literature, especially for phosphorus (Downing et McCauley, 1992; Jeppesen *et al.*, 2000a; Barnett et Beisner, 2007; Jeppesen *et al.*, 2000b; Orihel *et al.*, 2012; Monchamp *et al.*, 2014). In terms of macronutrients, nitrogen (N), mainly in the form of ni-

trate (NO_3), is one of the main nutrient inputs to lakes of the Koala Watershed as a result of mining activities, and more specifically from blast residue. Nitrogen inputs thus typically occur without addition of phosphorus (P), leading to a change in the N :P ratio in lakes, which in itself should have important effects on plankton communities (Saros *et al.*, 2012; Saros et Anderson, 2015). For example, the global shift toward a greater propensity for cyanobacteria blooms in lakes has been attributed not only to increases in macronutrient concentrations, but to altered N :P ratios (Paerl et Otten, 2013). Changes in phytoplankton composition in response to altered macronutrient stoichiometry should also trigger changes at the primary consumer (i.e. zooplankton) trophic level, and eventually potentially to higher trophic levels (e.g. fish), which respond to changes in size structure, quality or overall quantity of zooplankton.

We examined the impact of almost two decades of mining activity on the northern lake plankton communities downstream from Canada's first diamond mine using 19 years time series across five impacted and two reference lakes. We wanted to determine whether there has been a significant effect of mining activities, via water quality changes, on plankton functional composition and size structure, and to identify the drivers of community change.

4.3 Materials and methods

4.3.1 Study design and sampling

The Ekati Diamond Mine is located 100 km north of the tree line in the Canadian subarctic (64.71°N, 110.62 °W, Northwest Territories) on a landscape of interconnected wetlands and lakes (Figure 4.1, Table 4.1). Lakes in this watershed (Koala) are generally clear with low nutrient concentration and low productivity (Rescan, 2012). This study was conducted in five monitored lakes of the Koala Watershed, downstream of the mine's Long Lake Containment Facility (LLCF),

Tableau 4.1 Geographic coordinates of the study lakes and their morphometric characteristics.

Type	Lake	Lat.	Long.	Maximum depth(m)	Minimum depth(m)	Area (m2)	Shoreline (m)
Proximal	Leslie(Le)	64.68	-110.67	13	5.8	6.2×10^5	6.8×10^3
	Moose(Mo)	64.68	-110.65	9.9	1.5	4.4×10^2	5.4×10^3
Distal	Nema(Ne)	64.68	-110.72	9	1.9	7.8×10^5	8.0×10^3
	Slipper(Si)	64.61	-110.85	16	3.2	1.9×10^6	1.5×10^4
	S2	64.61	-110.84	35	11.5	1.4×10^8	1.4×10^5
Reference	Nanuq(Na)	64.92	-110.28	28.5	8.9	3.1×10^7	1.1×10^4
	Counts(Co)	64.65	-110.29	15.5	4	1.2×10^6	6.3×10^3

which receives mining by-products such as processed kimberlite, as well as all water that has been used in mining activities. The LLCF is considered to be the main influence of the mine on the surrounding aquatic environment, as water meeting regulatory effluent criteria is periodically discharged downstream into Leslie Lake Rescan (2012). Consequently, we expected to observe a decrease in detectable mine effects through the downstream watershed, as distance from the LLCF increased. To do so, we divided monitored lakes in two categories : lakes that were proximal to the LLCF (Leslie and Moose) and distal lakes (Nema, Slipper and S2). We compared the monitored Koala Watershed lakes to two reference lakes outside of the Koala Watershed to track natural temporal trends in subarctic lakes.

Plankton communities were sampled annually, in early August, at the deepest point in each lake. Phytoplankton were sampled at 1m with a Teflon-lined General Oceanics FLO bottle (GO FLO ; 5 L) and whole water samples were preserved in Lugol's iodine solution. Zooplankton (crustacean and rotifer) were sampled using vertical hauls of a conical 118 µm mesh net (0.3m diameter) equipped with a General Oceanics flowmeter (Model 2030R). Zooplankton were preserved in 5%

buffered formalin (final concentration). For phytoplankton and zooplankton, three samples were collected and averaged for further analyses. Zooplankton counts were done on a series of 1 ml subsample aliquots that were counted sequentially until the target count of between 200 and 400 crustacean and rotifer zooplankton were identified. Organisms were identified to the most highly resolved taxonomic level possible. For phytoplankton, the volume of sample enumerated was dependent on overall cell densities. The subsample was mixed and allowed to settle in an Utermohl-type settling chamber for approximately 24 hours and then examined and enumerated at 630x magnification using an inverted Leica microscope. Phytoplankton were identified to the lowest practical taxon using the transect method until at least 300 natural counting units were enumerated. For colonial algae, each colony was counted as one natural unit and cell numbers in each unit were recorded, or in the case of filaments, each filament was counted as one natural unit and the cell numbers of each filament were recorded (for details see ERM, 2014). Environmental variables were measured at the same time as the plankton sampling. Water quality samples were collected at 1m using an acid-cleaned, Teflon-lined General Oceanics FLO bottle. All water quality samples were sent to ALS Global (Yellowknife, NWT) for analyses of water quality variables at the lowest available detection limit (for details see ERM, 2014).

4.3.2 Response variables : Functional composition and size structure

The overarching objective of this study was to use a functional trait approach (functional composition and size structure) to understand the ecological implications of observed changes in the plankton communities of monitored lakes in the Koala Watershed, as well as the reference lakes. The selection of functional traits was thus critical for obtaining ecologically meaningful results. Selected traits for phytoplankton and zooplankton (rotifer and crustacean) were chosen to reflect how organisms interact with their environment (response or effect traits,

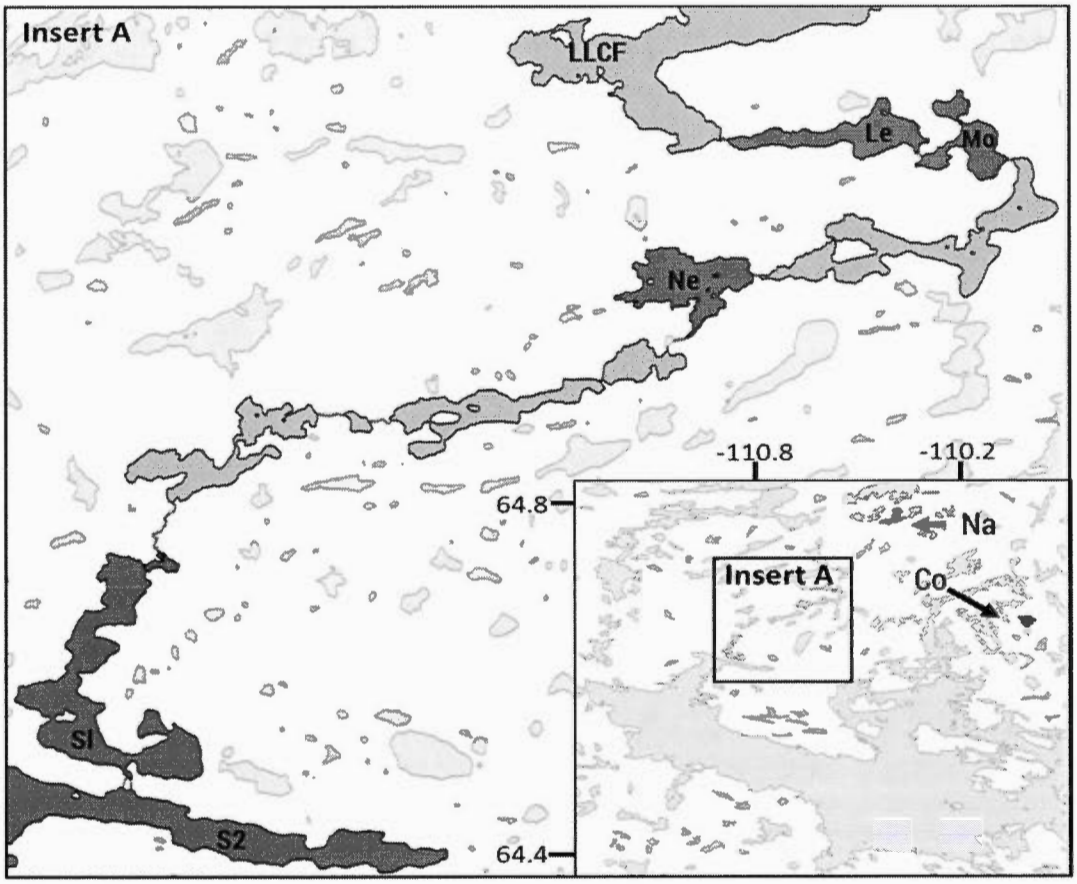

Figure 4.1 Map of the lakes showing the LLCF proximal lakes : Leslie (Le) and Moose (Mo), and the distal lakes : Nema (Ne), Slipper (Sl) and station 2 of Lake de Gras (S2) in the Koala Watershed. Nanuq (Na) and Counts (Co) from a nearby watershed were reference lakes.

see Hooper *et al.*, 2005). Thus, we selected traits related to resource acquisition (e.g. pigment type, feeding strategy) and predation avoidance strategies (e.g. motility, relative swimming speed), as these functional traits are those that establish the trophic relationships in food webs, including responses to nutrient enrichment (Table 4.2). Phytoplankton trait values were obtained from the literature (see Longhi et Beisner, 2010, for details) and included traits related primarily to resource acquisition : (i) capacity for N-fixation, (ii) silica demand, (iii) capacity for mixotrophy, (iv) pigment composition; and to predator avoidance : (v) cell motility and (vi) edibility to zooplankton ($< 35\,\mu m$ maximum linear dimension) and (vii) tendency to form colonies. Crustacean zooplankton traits values were also obtained from the literature (see Barnett *et al.*, 2007) and included (i) feeding type, (ii) trophic group and (iii) relative swimming speed (RSS, categorical variable from 0 to 6 with 0 being relatively non-motile). Information on functional traits for rotifers is very limited relative to phytoplankton and crustacean zooplankton; the only available for comparison were morphological traits related to predator avoidance (see McCauley, 1984) : (i) shape, (ii) the presence of a spine and (iii) tendency to form colonies. With these traits, we estimated functional composition as our measure of functional change.

In addition, because size is known to be an important integrative trait (Litchman *et al.*, 2013) on resource acquisition and predation avoidance strategies, size structure was also used as an independent measure of functional change. Phytoplankton biomass was estimated from biovolumes using cell and colony dimensional length measurements and corresponding geometrical forms (Hillebrand *et al.*, 1999). Zooplankton (rotifer and crustacean) biomass was similarly estimated using McCauley (1984) and Culver *et al.* (1985).

To estimate functional composition, the relative presence (proportion) of each functional trait was calculated as the aggregated biomass of all organisms pos-

sessing a specific trait divided by the total community biomass. For this study, organisms were identified at the species level when possible; however, since many functional traits are conserved within families or orders, it would have been possible to do the same functional analyses using a coarser taxonomical resolution. To construct the size structure matrix, the entire size range of phytoplankton, rotifer and crustacean zooplankton was divided into ten logarithmic size classes and the proportion of total biomass in each class was calculated. The mean maximum linear dimension (MLD) of each plankton species were measured in 2014 and these values were then applied across all years. Literature values were used to supplement species that were absent from 2014 samples. This approach precluded examining intra-specific size variation but provided a coarse picture of size structure in the plankton communities. For phytoplankton, a further limitation of this approach was that size structure was based on single-cell biovolumes without information on overall colony size as many colonies are destroyed in Lugol's. Thus, with respect to edibility by zooplankton based on unit size, we have likely underestimated size structure influences of phytoplankton (i.e. conservative estimates).

4.3.3 Potential driving variables

Another objective of this study was to link changes in plankton functional structure to environmental variation, to identify the likely drivers of the observed functional changes. Because plankton may respond to variation in different ecosystem properties, we divided potential drivers into four main categories : morphometric variables (mean depth and lake area), physical variables (mixing depth, secchi depth, stability and water column temperature), water quality variables and biotic variables (Table 4.3). Morphometric variables (Table 4.1) were not influenced by mining activities and thus represented a pure lake identity effect : testing whether lakes with different morphometries had intrinsically different functional composition and size structure. Mean depth was calculated using bathymetric surveys

Tableau 4.2 Phytoplankton, rotifer and crustacean zooplankton functional traits and levels.

	Category	Traits	Values
Crustacean zooplankton	Resource acquisition	Trophic position	Carnivore Omnivore-Carnivore Omnivore Omnivore-Herbivore Herbivore Immature
		Feeding type	B (*Bosmina*)-filtr. C (*Chydorus*)-filtr. D (*Daphnia*)-filtr. S (*Sidae*)-filtr. Stationary Suspension Raptorial
	Predation avoidance	Relative swimming speed (RSS)	0(slow) - 6(fast)
Rotifer	Predation avoidance	Shape	Cone Cyclinder Ellipsoid Parallelepiped
		Spines	yes/no
		Colonial	yes/no
Phytoplankton	Resource acquisition	Nitrogen Fixation	yes/no
		Si requirement	yes/no
		Mixotroph	yes/no
		Pigments	Green Blue Brown Mixed
	Predation avoidance	Motility	None Flagellated Vacuole
		Edible	yes/no
		Colonial	yes/no

and lake area estimated from areal photos or topographic databases using GIS software. Second, lake physics as represented by thermal stratification structure and water column stability can impact plankton community functional composition given that plankton are drifting organisms. Variation in a lake's physical properties may be related to mining activities or to changes occurring at larger scales (e.g. climate warming). Mixing depth and water column stability were estimated from temperature profiles using the R package : Lake Analyzer (Read *et al.*, 2011) . Water column temperature was estimated as the mean temperature over the entire water column. The third group of variables encompassed water quality and were likely to be the main effects of mining activities on downstream lakes, via the influence of several chemical variables (see ERM, 2014) . To characterize water quality, we relied on traditional limnological water quality variables related to important macronutrients (i.e. nitrogen and phosphorus) and pH, turbidity, conductivity, alkalinity, dissolved solids and water hardness as well as potentially toxic compounds (Appendix Table 4.6). Water quality variables were averaged annually, and missing values were replaced by linearly interpolating the preceding and following years. For statistical analyses, we reduced the number of water quality variables and established the main axes of variation by using the first two principal components (PC1 and PC2) of a Principal Components Analyses (PCA ; Appendix Figure 4.8 and Table 4.6). The main axes of variation in water quality with respect to mining activities were thus represented by an increase in nitrogen (i.e. NO_3, $NO2$ and NH_4), water hardness, conductivity, and pH (PC1) with PC2 being related to phosphorus (TP and orthophosphate), metals and turbidity. Finally, because plankton communities do not respond solely to abiotic variables, we also included potential biotic driving variables to account for interaction between the trophic levels. As done for the environmental variables, we used PC1 and PC2 of a "biotic" PCA to capture the main axes of variation in functional trait composition in the other trophic level (phytoplankton for crustacean zooplankton

Tableau 4.3 Variables used in the RDA as response and explanatory variables. "Other communities" refers to the principal components (PC1 and PC2) associated with PCAs done on all taxa excluding the focal community in each case (see Appendix S1 : Tables S2, S3, S4 and Figure S2, S3 and S4). Z refers to depths of : mean lake (Mean Z), mixed layer depth (Zmixed) and secchi depth (Zsecchi).

Response variables	Explanatory variables			
Composition	Morphometry	Physical	Water Quality	Biotic
Functional composition	Mean Z	Z mixed	PC1	PC1 & PC2 other communities
	Lake Area	Z secchi	PC2	
		stability		Biomass other communities
		temperature		

and rotifer and vice-versa, Appendix Tables 4.7, 4.8, 4.9 and Figures 4.9, 4.10, 4.11).

4.3.4 Testing the effect of mining activities on plankton (PERMANOVA)

To test whether the effect of mining activities on plankton functional composition and size structure was significant, we used PERMANOVA, the permutational multivariate version of ANOVA, (Anderson, 2001). We first tested the hypothesis that there was no significant interaction between lake Type (monitored vs reference) and Year (Time) on several response variables. If there was a significant Type*Year interaction, it would mean that functional differences between monitored and reference lakes changed through time, indicating an effect of mining activities. Response variables in the PERMANOVA model were functional composition, and size structure. Because we expected the effect of mining activities to be greatest in lakes that were closer to the LLCF, following a significant monitored vs. reference difference, we then compared separately each group of lakes (proximal Leslie and Moose or distal Nema, Slipper and S2) to the reference lakes in a second set of PERMANOVAs to detect whether responses to mining activi-

ties were different or delayed between these . P-values were obtained using 999 permutations under a reduced model constrained within lakes. Our unbalanced statistical design (i.e. five monitored and two reference lakes) could affect rejection rates in the PERMANOVA (Anderson and Walsh 2013), especially when all lakes are considered. Depending on which group of lakes had the largest variance, the PERMANOVA could either be too liberal or too conservative (Anderson and Walsh 2013). To compare the variance between reference (2) and monitored (5) lakes we used the betadisper function (vegan R library, Oksanen et al. 2015), and in all cases the variance between monitored lakes was more important than the variance between reference lakes. This indicates that the p-values of the PERMONOVA were conservative. In the PERMANOVAs comparing proximal (2) or distal (3) lakes to reference lakes (2), the design was almost balanced, leading to a less biased rejection rate.

4.3.5 Visualizing temporal trends in functional structure (Principal Response Curves)

When the interaction between Type and Year was significant (i.e., when an effect of mining activities was identified), multivariate techniques were used to visualize how the response was structured through time and to identify the drivers of the response. We expected the response to mining activities to be structured temporally, such that differences between lakes in the PERMANOVAs would increase with time. We used Principal Response Curves (PRCs) to (i) visualize the community functional response through time and (ii) to identify which functional traits and size classes responded the strongest. PRCs were conducted only when the effect of mining activities was statistically significant ($p < 0.05$) in the PERMANOVA. Visualizing temporal trends with multivariate data using standard ordination techniques (e.g. PCA, RDA) is challenging because in ordination plots, sites will not often be organized in a chronological fashion (van den Brink et

al. 2009). PRCs, an extension of RDA (using the equation : Response Treatment x Time + condition(Time)), is a statistical technique that enables the explicit representation of sites in a chronological order and graphically illustrates the temporal deviation of monitored from reference lakes by constraining the ordination using the interaction between treatment Type (monitored versus reference) and Year. In the context of the present study, PRC analysis was used to identify if and when the functional composition and size structure of monitored lakes began to deviate from those of reference lakes and to determine whether the timing of the response was related to the distance from the mine (by comparing the proximal vs. distal responses). In PRC diagrams, the effect (displayed on the y-axis) is the first principal component of the treatment effect over time (displayed on the x-axis), which represents the difference of the overall functional response of communities in monitored lakes compared to reference lakes (the zero line). Only the first PRC axis was retained in all cases. All PRCs were performed using the prc function (vegan R library, Oksanen et al. 2015). PRCs also allowed for the identification of which traits, size classes were responsible for the differences between monitored and reference lakes and consequently those that responded to mining activities by using PRC "species" weights. As with such scores in other ordination techniques, the relative magnitude of the "species" weights represents how strongly a group (a trait in this case) loads onto the PRC axis, and thus represents the strength of the response by a specific trait (in this case). Also, the sign (+/-) associated to the weight represents whether the response was positive or negative relative to the control (reference) condition. Thus, traits with high absolute weights are the traits that mainly explain the functional difference between monitored and reference lakes. PRC analyses were also conducted on the taxonomic data and compared to the PRC analyses for functional traits to determine whether similar patterns were observed by the two approaches.

4.3.6 Identifying drivers

Finally, to confirm that the observed responses were the result of mining activities, we investigated the drivers of the functional changes in plankton using redundancy analysis (RDA) and variation partitioning. As potential explanatory variables we used water quality parameters (water quality PC1 and PC2) along with the other potential environmental drivers including the morphometric, physical, and biotic variables. We then partitioned the variance explained by the groups of variables (water quality, physical, morphometric and biotic) to better understand the potential sources of variation in plankton functional composition and size structure. However, because no variation was independently explained by physical variables in any variation partitioning, we only used water quality, morphometric and biotic variables (see Figure 4.3) to simplify interpretation.

4.4 Results

4.4.1 Effects of mining activities on lake plankton

The effect of mining activities (Year*Type in PERMANOVA) on phytoplankton functional composition and size structure was significant for proximal and distal lakes when compared to reference lakes (Table 4.4 ; main effects are in Appendix : Table 4.5). For rotifers the effect of mining activities on functional composition and size structure was significant (Table 4.4). Finally, for crustacean zooplankton, the effect of mining activities on functional composition and size structure was significant both in proximal and distal lakes compared to reference lakes (Table 4.4).

4.4.2 Responses of plankton communities to mining through time

The phytoplankton functional composition response curves (PRC) showed a clear temporal divergence of monitored lakes from reference lakes (horizontal vs. other

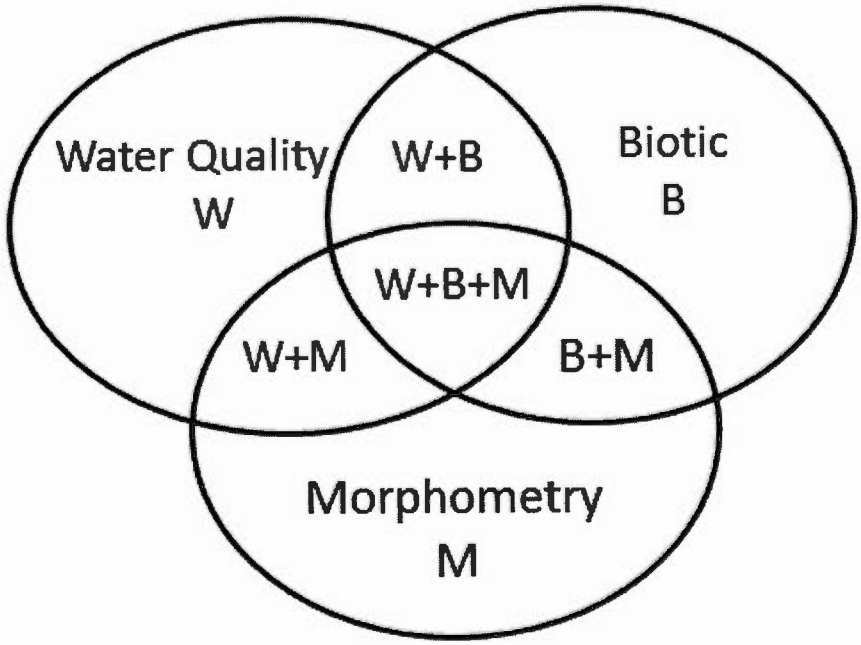

Figure 4.2 Venn diagram showing the structure of the variation partitioning analyses. Results for each fraction are shown in Table 5

Tableau 4.4 Simplified PERMANOVA table, the interaction of *Year*Type* test for the significance of mining activities composition and size structure. Based on 999 permutations. See Table S-1 for the full PERMANOVA table.

		Overall			Proximal			Distal		
		SS	F	p	SS	F	p	SS	F	p
Phytoplankton	Functional traits	1.1	4.2	0.005	2.2	5.4	0.007	1.5	3.8	0.04
	Size classes	3.4	2.9	0.03	4.8	4.8	0.018	3.0	3.3	0.07
Rotifer	Functional traits	1.2	3.4	0.045	2.0	16.8	0.001	1.0	3.8	0.07
	Size classes	2.5	2.6	0.17	5.8	18.0	0.002	2.1	3.7	0.10
Crustacean	Functional traits	2.8	3.5	0.002	3.9	10.7	0.003	2.6	3.8	0.009
	Size classes	3.8	3.8	0.003	4.5	9.1	0.005	3.6	3.8	0.02

lines in Figure 4.3a). Moreover, the timing of the functional composition response was proportional to the distance from the mine : the closest lake (Leslie) responded first, followed by Moose, and Nema. Slipper responded after 2005, while S2 only started to respond in 2010. Although differences between monitored and reference lakes were significant through the whole sampling period, the divergence in functional composition between these lakes clearly increased with time. Furthermore, following the initial responses in Leslie, Moose, and Nema (lakes proximal to the LLCF), the functional divergence of phytoplankton appears to have stabilized around the same level of difference from reference, despite variation in the downstream distance from the LLCF. Monitored lakes had greater biomass of edible and non-motile phytoplankton, and with high silica demand (Figure 4.3a), with decreases over time in mixotrophic, flagellated and colonial phytoplankton traits. The size structure PRC displayed the same general pattern as for functional composition, with shifts first appearing and being stronger in proximal lakes (Appendix Figure 4.12). However, one important difference was that between 2010

and 2013, size structure in Leslie and Moose size structure reversed temporarily. Which could be explained by a shift from a smaller species, *Cyclotella*, to a larger one, *Puncticulata* (data not shown). However, because these two species have the same functional traits (they are both small centric diatoms) this shift was not observable in functional composition. Finally, the temporal pattern displayed by phytoplankton taxonomic composition (Appendix Figure 4.12) was also almost identical to functional composition, with *Cyclotella*, *Cryptomonas* and *Dinobryon* responding the most.

For rotifers, prior to 2009, the first PRC axis of functional composition showed mainly differences between distal lake S2 and the other lakes indicating lake-specific differences (Figure 4.3b). It was only after 2009 that a clear divergence of proximal lakes from reference and distal lakes occurred (Figure 4.3b). The functional composition divergence occurred later for rotifers than for phytoplankton, and does not have appear to have stabilized. The observed functional response in proximal lakes (Figure 4.3b) was a shift from conical species (predominantly of the genus Kellicotia) to parallelepiped species (predominantly of the genus *Keratella*, see Appendix : Figure 4.13). Similar responses were observed in the rotifer size structure PRC, with shifts to smaller species in Leslie and Moose occurring after 2009. In each rotifer PRC, Nema and Slipper diverged from reference lakes in 2012, but in a different direction than Leslie and Moose (Figure 4.3b and Appendix : Figure 4.13). This divergence was not the result of functional compositional shifts in Nema and Slipper but was rather the result of a change in reference lake rotifer composition (i.e. the zero line). The temporal pattern displayed by rotifer taxonomic composition (Appendix : Figure 4.13) was more similar to that for size structure than for functional composition. In S2 there was important annual variation in the proportion of *Asplanchna*, a very large rotifer, while proximal lakes shifted from being dominated by *Kellicottia*, a species with long protective spines,

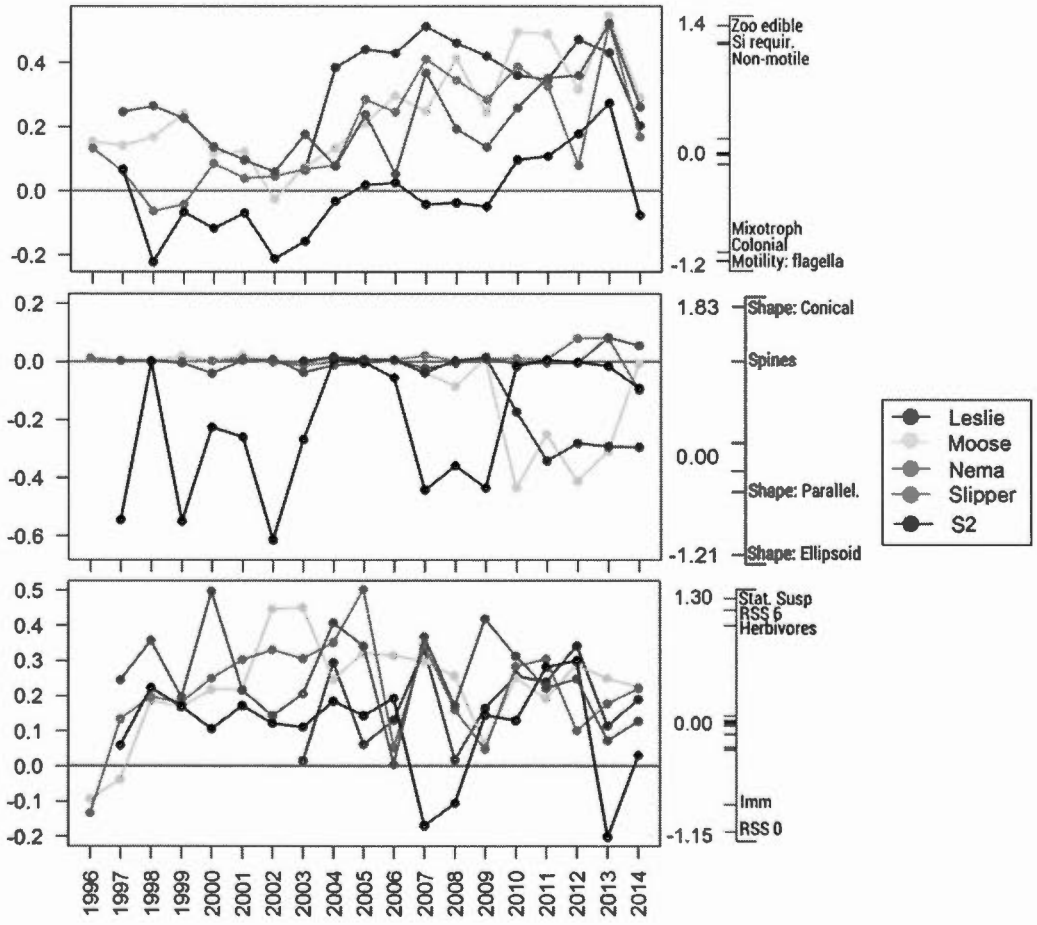

Figure 4.3 Principal Response Curves (PRC) for functional composition of : (a) phytoplankton, (b) rotifers, and (c) crustacean zooplankton in the monitored lakes (Leslie, Moose, Nema, Slipper and S2) vs. reference (Nanuq and Counts; the 0 line) lakes. Weights show the degree to which functional traits responded to mining activities. For clarity, only traits with an absolute weight > 0.5 are shown.

to *Keratella* a species that has shorter spines.

For crustacean zooplankton, despite a significant effect of Year*Type detected in the PERMANOVA analyses, there was no directional temporal pattern in the differences between monitored and reference lakes, and no clear functional shift through time (Figure 4.3c). Together, these results suggest that reference and monitored lakes are functionally different a priori with respect to their crustacean zooplankton communities and that an added effect of mining activities was not additionally detectable. In general, monitored lakes had greater abundances of herbivores, fast swimming (RSS6) stationary suspension feeders, characterized taxonomically by species within the Calanoida order, with lower relative dominance of slow swimming taxa and immature stages. Similarly, size structure varied between monitored and reference lakes, but without a clear temporal pattern (Appendix : Figure 4.14). Medium-sized crustacean zooplankton were most dominant in the monitored lakes. Temporal patterns in crustacean zooplankton taxonomic composition were similar to both functional and size structure trends, again, with no clear temporal pattern (Appendix : Figure 4.14).

4.4.3 Drivers of the functional response

Redundancy analyses were only performed on the functional composition data because the size structure responses were similar to the functional ones through time (PRC analyses). For phytoplankton functional composition most of the variation, 47% of total and 89% of constrained variation in the RDA (Figure 4.4), was explained by the first axis. Functional traits loading strongly on this axis were the same as those identified in the PRC (Figure 4.3a). Water quality PC1 (WQ PC1) loaded strongly on RDA axis 1, along with PC1 of crustacean zooplankton (Crust PC1), which also loaded positively on the first axis. On the other hand, lake morphometric variables (Mean Z and log.Lake Area) loaded negatively on

the first axis, while physical variables (WC stability) loaded positively. Most of the explained variation in the phytoplankton functional RDA was independently explained by water quality (23%, $p<0.0001$;Table 4.5). All the variation explained by morphometry was shared with water quality, biotic variables or both. A highly significant ($p=0.001$) 6% fraction of the variation was also independently explained by biotic variables.

For rotifer functional composition, the first axis explained 33% and the second 13% of the variation in the RDA (Figure 4.5). Morphometry (Mean Z and log.Lake Area) and water quality PC1 (WQ PC1) had strong loadings on the first two axes, while crustacean PC2 (Crust PC2) loaded on the first axis and phytoplankton PC1 (Phyto PC1) on the second. The importance of lake area was consistent with the observation that S2, a large lake, was functionally different, dominated by ellipsoid species. Parallelepiped rotifers were associated to changes in water quality. Variation partitioning demonstrated that lake morphometry independently explained a large and significant (16%, $p<0.0001$; Table 4.5) amount of the variation in the RDA. Water quality (17%, $p<0.0001$) and biotic variables (6%, $p=0.001$), also significantly independently explained variation in rotifer functional composition.

The first axis of the crustacean zooplankton functional composition RDA explained 23% of the total variation and the second 9% of the constrained variation (Figure 4.6). On the first axis, water quality PC1 (WQ PC1), morphometric (mean Z), physical (Secchi Z and Thermocline Z), and biotic variables (Phyto PC1 and Phyto PC2) had strong loadings. As observed for phytoplankton and rotifers, the functional traits that loaded strongly on the first axis were the same that responded in the PRC (i.e. Stat. susp., RSS 6, RSS 0 and Immature). Along the weaker second axis, rotifers and crustacean traits of carnivory and raptorial feeding loaded. One important difference in the variation partitioning (Table 4.5), was that water quality variables independently explained only 2% of the varia-

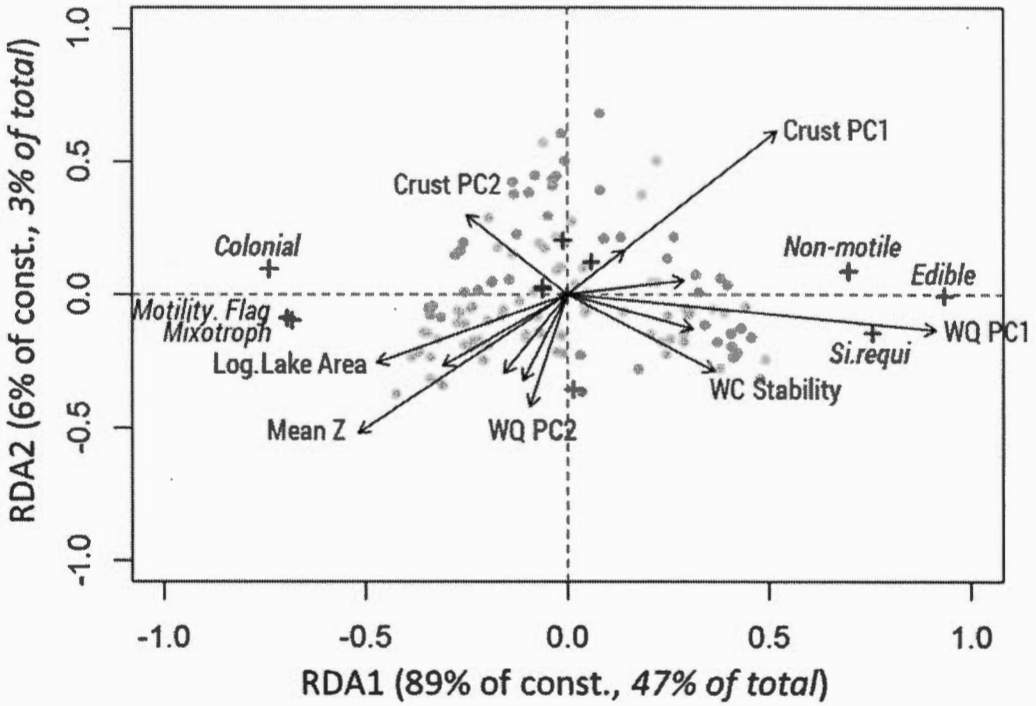

Figure 4.4 Ordination diagram of the phytoplankton functional composition RDA. Functional traits (response variables) are represented by crosses, and environmental variables (explanatory variables) by arrows. On each axis, constrained (const.) and total explained variation is reported. The unlabelled arrows correspond to the following variables starting in quadrant 1 (closest to 12 :00 on a clock) and moving in a clockwise direction : WC temperature, Biomass crustacean, Rotifer PC2, Rotifer PC1, Thermocline Z, Biomass rotifer and Crustacean PC2.

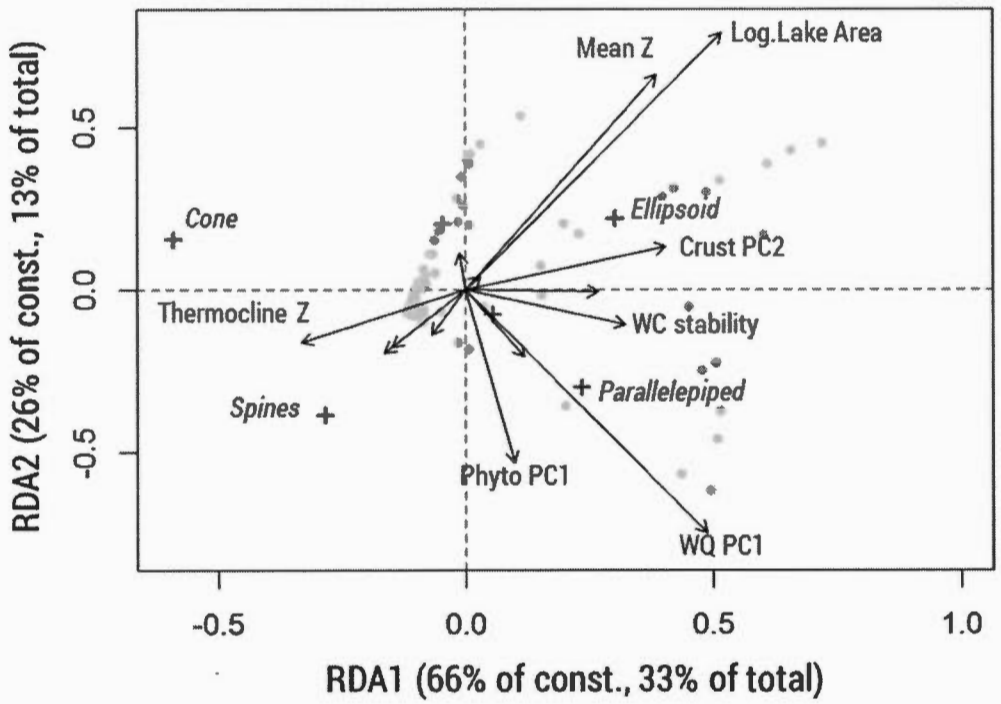

Figure 4.5 Ordination diagram of the rotifer functional composition RDA. Functional traits (response variables) are represented by crosses and environmental variables (explanatory variables) by arrows. On each axis, constrained (const.) and total explained variation is reported. The unlabelled arrows correspond to the following variables starting in quadrant 1(closest to 12 :00 on a clock) and moving in a clockwise direction : WQ stability, Secchi depth, Biomass phytoplankton, Crustacean PC1. Phytoplankton biomass, phytoplankton PC2, WC temperature and WQ PC2.

Tableau 4.5 Adjusted R^2 values from the variance partitioning on functional composition by plankton group shown as percentages for each fraction, as defined in Figure 2. Only the W, B and M fractions were statistically testable with significance (p-values) corresponding to * p<0.05, ** p<0.001 and *** p<0.0001.

	W	B	M	W+M	W+B	B+M	W+B+M
Phytoplankton	*** 0.23	** 0.06	0	0.03	0.05	0.03	0.08
Rotifer	*** 0.17	** 0.06	*** 0.16	0	0.03	0.04	0
Crustacean zooplankton	* 0.02	*** 0.08	*** 0.1	0.02	0.03	0.02	0.05

tion (p=0.01), while biotic and morphometric variables independently explained 8% and 10% of the variation (p<0.0001 for both). The variation independently explained by water quality was low, but could be more important because of the shared variation with morphometry and biotic variables.

4.5 Discussion

The aggregate effects of diamond mining activities on the functional composition and size structure of the plankton communities in the focal northern Canadian watershed were significant across community types. The response to mining activity of phytoplankton and rotifer communities had a strong temporal structure and was sequential : functional changes occurred first in proximal lakes, followed by distal lakes. The functional composition response in phytoplankton was strongly linked to water quality and appeared many years before that of the rotifers, suggesting a bottom-up progression of effects. The long-time-lag between the responses of the different trophic levels, occurring over several years was surprising considering that plankton organisms have very short generation times and can thus respond

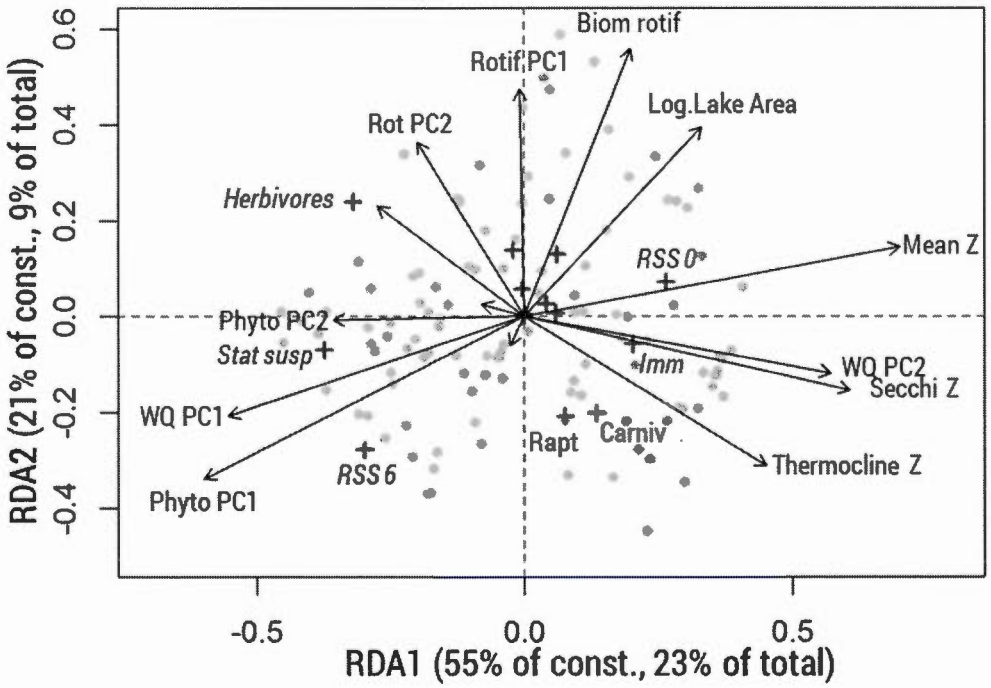

Figure 4.6 Ordination diagram of the crustacean zooplankton functional composition RDA. Functional traits (response variables) are represented by crosses, and environmental variables (explanatory variables) are represented by arrows. On each axis, constrained (const.) and total explained variation is reported. The unlabelled arrows correspond to the following variables starting in quadrant 1 (closest to 12 :00 on a clock) and moving in a clockwise direction : WQ stability and Biomass phytoplankton.

rapidly to a changing environment (McCormick et Cairns, 1994; Stemberger et Lazorchak, 1994). A community response in the crustacean zooplankton was less obvious, and although there was a significant effect on functional composition and size structure in the PERMANOVA, no directional temporal patterns in functional change in the crustacean zooplankton community were observed in the PRCs. The lack of a temporal directional trend suggests that the observed differences between monitored and reference lakes were year-specific rather than related to mining activities.

In the phytoplankton, although they responded strongly, traits related to edibility (edibility, motility, free-living) were probably not the only ones under selection, as the phytoplankton functional composition in monitored lakes shifted toward small centric diatoms, a functional group that can be favoured when unproductive lakes are enriched with nitrogen (see Saros et Anderson, 2015, for a review). Although we cannot directly attribute the response of phytoplankton to N-enrichment, it is the most plausible explanation given the perturbation applied by the mining activity, and accords with recent evidence demonstrating that small centric diatoms respond to this factor (Saros *et al.*, 2012,0). On the other hand, the effect of lake thermal structure was not significant, although it has also been identified as a driver of small centric diatom abundance in northern lakes (see Rühland *et al.*, 2015, for a review). The strong response we observed in traits related to phytoplankton edibility should favor a bottom-up trophic response of zooplankton.

Rotifer communities also shifted toward smaller species (mainly Keratella), and these shifts were related to nutrient (mainly N) enrichment. In the Great Lakes, a similar shift from Kellicottia dominance under oligotrophic conditions, to Keratella under eutrophic conditions has also been observed (Barbiero et Warren, 2011). The response of rotifer functional composition to changes in phytoplankton and crustacean zooplankton functional composition also validates the presence of

a trophic response. However, the restricted amount of functional knowledge on rotifer species in the literature limits the ecological interpretations we can draw for this group.

Given the shift toward more edible and accessible (non-colonial, non-motile) phytoplankton biomass, we would expect highly competitive crustacean zooplankton (i.e. large, filter-feeding cladocerans) to dominate (Lampert et Schober, 1980). Furthermore, diatoms are of high nutritional quality (Brett et Goldman, 1997), especially for herbivorous filter-feeders (Richman et Dodson, 1983). However, we did not observe a concomitant shift toward herbivorous filter-feeding cladocerans, but instead an increased dominance by the functional traits reflecting the calanoid copepods; the group that had already dominated prior to mining onset. One potential explanation for the absence of a shift toward filter-feeders could be that while food quantity and quality increased, phytoplankton concentrations (average of 742 cells/ml, Figure 4.7) were almost always under or close to the lowest concentration limit for cladocerans established at 1000 cells/ml (see Lampert et Schober, 1980), except in Nema where the average was 2732 cell/ml (Figure 4.7). Consequently, calanoids would have maintained a competitive edge with their lower food concentration limit (McNaught, 1975). Because cyclopoid copepods are one of the main predators of planktonic rotifers (Williamson, 1983), we also expected a response of crustacean zooplankton to functional changes in the rotifer community, especially if a shift in potential edibility was observed. Although, both Kellicottia and Keratella are common prey for many copepod species (Williamson, 1983), and the fact that we observe a negative relation between rotifers and raptorial and carnivorous zooplankton in the crustacean zooplankton RDA (Figure 4.6 Axis 2), the functional shift in rotifers with mining, did not affect overall community edibility in a way that influenced the primary crustacean zooplankton response (Figure 4.6 Axis 1). In this RDA and in the variation partitioning, changes in water quality

resulting from mining (WQ PC1) had small but significant effects on crustacean zooplankton functional composition, indicating only minor effects of mining activities on crustacean zooplankton. Given that during the implementation of mining activities there were non-directional changes in crustacean zooplankton functional composition and size structure, there is little evidence to indicate that crustacean zooplankton community composition in the studied lakes are related to the mine. Instead, the original community composition appears to have been reinforced in lakes impacted by mining activity. Thus, with respect to bottom-up effects propagating through the food web, mining effects on fish are likely to be minor as well. However, a full assessment of the fish communities would also need to be done to determine this more definitively, as there could be direct effects on fish that are beyond the influence of the food web.

By using a functional approach, we successfully synthesized shifts at the taxonomic level : taxonomic composition principle response curves were highly similar to those for functional composition and size structure for all groups. It is also interesting to note that for phytoplankton, functional composition better tracked taxonomic changes than did size structure; this could have resulted from the bias in our estimates of phytoplankton sizes for which, as colony size was not available. The limited functional information for rotifers may explain why the size structure and taxonomic compositions were more related than was functional composition. Overall, the functional approach offers promise to lake management in that it can reflect taxonomic and size shifts in plankton communities in response to environmental change.

Changes in water quality as a result of diamond mining activities have caused a functional shift in phytoplankton and rotifer communities in the lakes downstream of the mine. However, there are strong indications that after almost 20 years of activity, the impact of mining has been restricted to the base of the

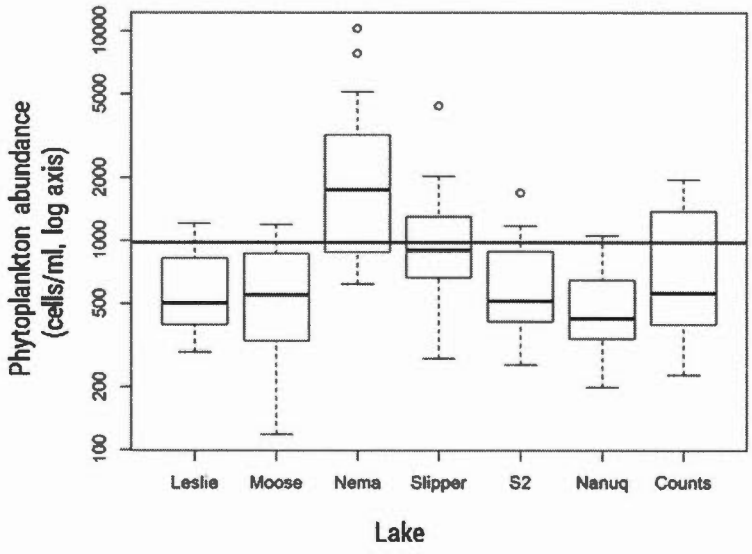

Figure 4.7 Boxplot of median total phytoplankton abundance in each lake. The red horizontal line represents the *Daphnia* lower food concentration limit according to Lampert (1980).

food web and that the functional structure of plankton communities is stabilizing over time. The weaker directional shift in crustacean zooplankton suggests minimal bottom-up effects are also likely for the fish communities in these lakes. For the mining industry, monitoring functional shifts in plankton traits composition at best, and size structure at minimum, will enable an excellent and potentially broadened understanding of the impacts of mining activities on aquatic communities. Classifying individuals more broadly into size classes or coarse taxonomic groups (i.e. genus or family rather than species) is usually sufficient to allow the implementation of a functional approach. Thus, this type of monitoring involves overall a smaller allocation of resources, expertise and time to classify taxa into functional groups. Our results show that it is likely to be a productive approach to assessing responses by aquatic communities to industrial perturbation and aid in environmental monitoring of lakes more generally.

4.6 Acknowledgments

Thanks to Erin Forster, Amy Elliott, Mark Nelson, Tom Jeffery, Laurie Ainsworth, Benjamin Beall, April Hayward, and Claudine Lee for help with the data collection, study design, and manuscript review. This research was funded by an Engage Grant (EGP 475781-14) from the Natural Sciences and Engineering Research Council of Canada (NSERC) to BEB. As part of its partnership in the Engage Grant, DDEC provided in kind contributions. ERM Consultants Canada Inc. provided logistical and technical support. Dominion Diamond Corporation (DDEC) collected the data and provided access to the databases.

4.7 Appendix

Tableau 4.6 Principle component (PC) loadings of the variables in the water quality PCA

Environmental variable	WQ PC1 loadings	WQ PC2 loadings
Conductivity	0.28	-0.05
Water Hardness	0.28	-0.04
Sulphate (SO_4)	0.28	-0.05
Barium (Ba)	0.28	-0.05
Alkalinity	0.28	-0.01
Nitrate (NO_3)	0.27	-0.1
Total Dissolved Solids (TDS)	0.27	-0.05
Uranium (U)	0.27	-0.05
Magnesium (Mg)	0.26	-0.03
Nickel (Ni)	0.26	0.03
pH	0.25	0.04
Ammonium (NH_4)	0.25	0
Nitrite (NO_2)	0.24	-0.07
Copper (Cu)	0.18	0.36
Turbidity	0.1	0.31
Aluminium (Al)	0.1	0.49
Total Phosphorus (TP)	0.05	0.38
Ortophosphate	-0.05	0.12
Iron	-0.06	0.58

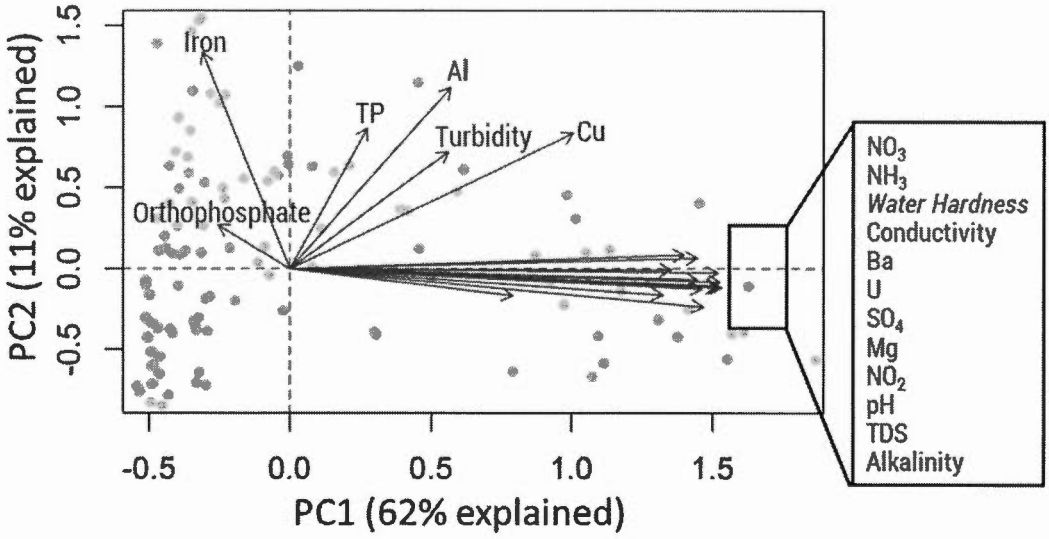

Figure 4.8 Biplot of the water quality PCA.

Tableau 4.7 Principle component loadings of the functional traits in the phytoplankton functional composition PCA

Biotic variable	PC1 loadings	PC2 loadings
Motility : Flagellated	-0.88	-0.37
Mixotroph	-0.85	-0.37
Colonial	-0.81	0.59
Nitrogen fixation	-0.03	0.14
Pigment : Blue	-0.03	0.14
Pigment : green	-0.01	0.51
Motility : Vacuole	0	0
Pigment : Brown	0.01	-0.64
Pigment : Mixed	0.03	-0.01
Non-motile	0.88	0.37
Si requirement	0.9	-0.28

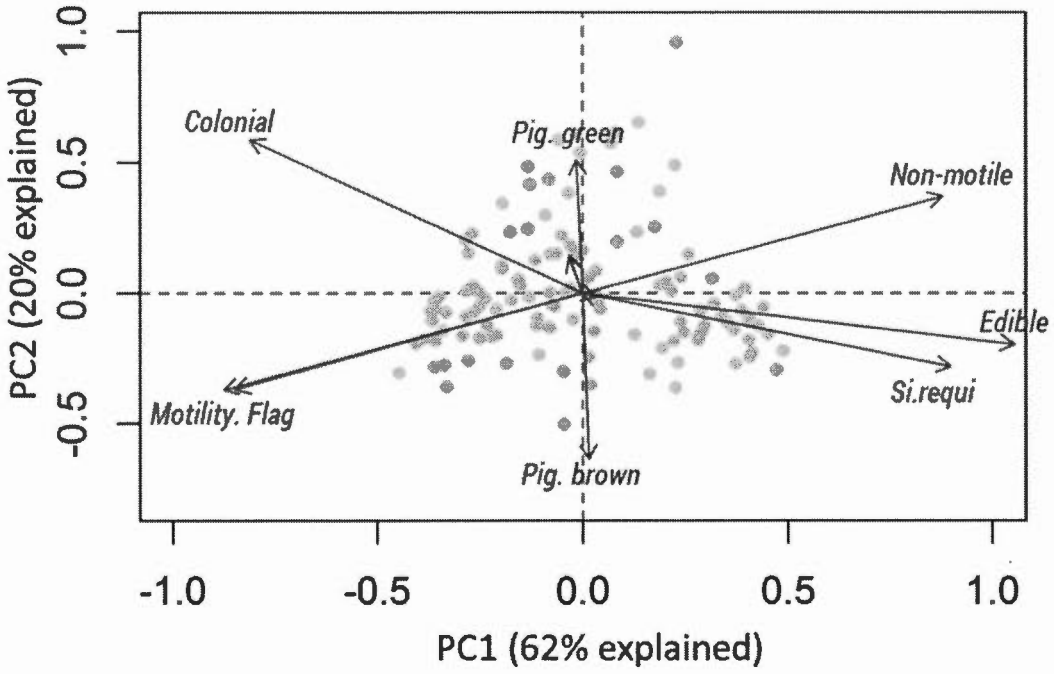

Figure 4.9 Biplot of the phytoplankton functional composition PCA.

Tableau 4.8 Principle component loadings of the functional traits in the rotifer functional composition PCA

Rotifer variable	PC1 loadings	PC2 loadings
No-Spines	-1.05	0.38
Shape : cone	-1	-0.81
Shape : cylinder	0.1	0.07
Shape : parallelepiped	0.17	0.58
Colonial	0.24	-0.55
Shape : ellipsoid	0.73	0.17
Spines	1.05	-0.38

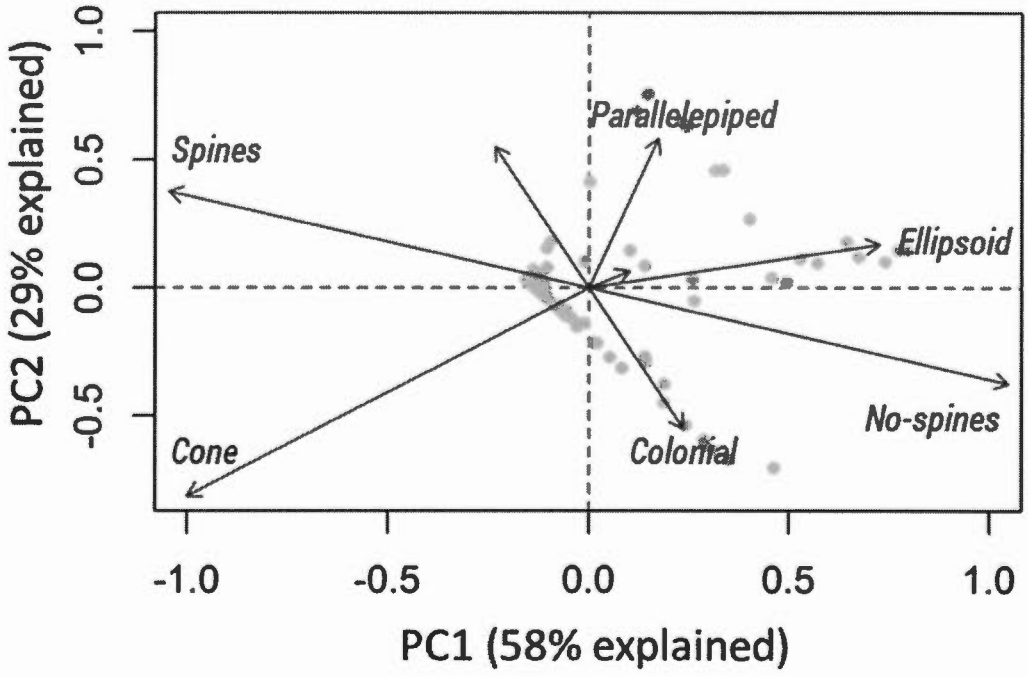

Figure 4.10 Biplot of the rotifer functional composition PCA.

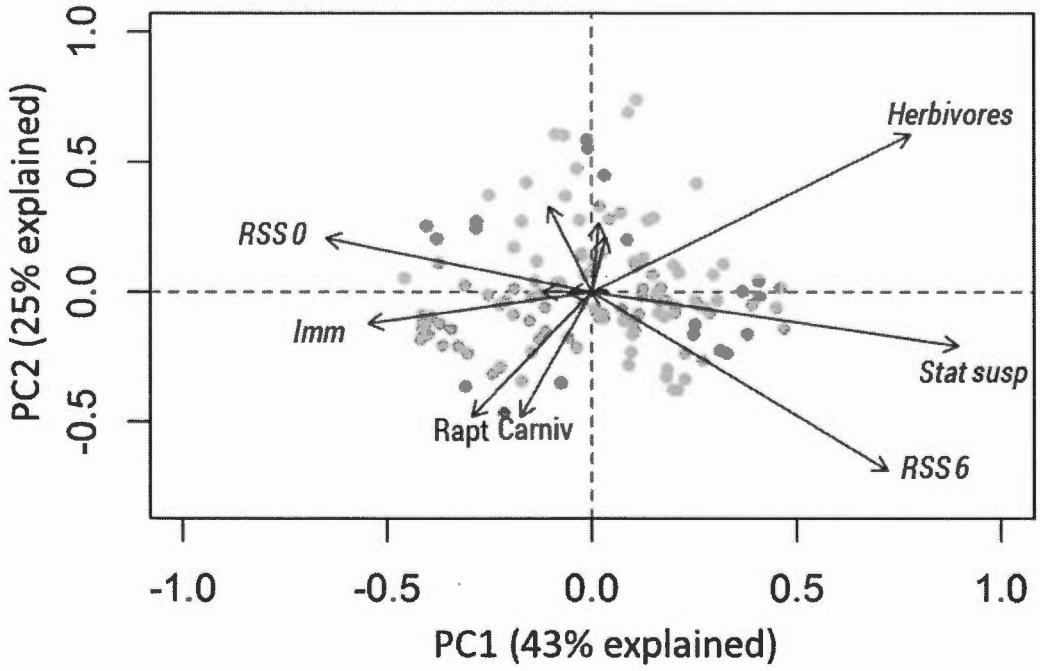

Figure 4.11 Biplot of the crustacean zooplankton functional composition PCA.

Tableau 4.9 Principle component loadings of the functional traits in the crustacean zooplankton functional composition PCA

Variable	PC1 loadings	PC2 loadings
RSS 0	-0.65	0.21
Immature	-0.55	-0.12
Raptorial	-0.29	-0.48
Carnivore	-0.17	-0.48
RSS 5	-0.12	0
S-filtration	-0.1	0.33
Omnivore-Carnivore	-0.06	0
C-filtration	0	0
RSS 1	0	0
RSS 3	0	0
D-filtration	0.02	0.27
RSS 4	0.02	0.27
B-filtration	0.03	0.21
RSS 2	0.03	0.21
RSS 6	0.72	-0.69
Herbivore	0.78	0.61
Stationary Suspension	0.9	-0.21

Tableau 4.10 Full PERMANOVA table, the interaction of Years*Type test for the significance of mining activities on phytoplankton functional community structure. Based on 999 permutations.

		Source	General				Proximal				Distal			
		of variation	df	SS	F	p	df	SS	F	p	df	SS	F	p
Phytoplankton	Functional traits	Year	6	6.0	63.3	0.001	3	5.7	79.3	0.001	4	3.8	42.0	0.001
		Lake	17	3.3	11.3	0.001	17	2.4	5.9	0.001	17	3.0	7.7	0.001
		Year*Type	17	1.1	4.2	0.005	17	2.2	5.4	0.007	17	1.5	3.8	0.04
		Residuals	318	5.0			160	3.8			230	5.25		
	Size classes	Year	6	10.6	25.9	0.001	3	7.5	43.2	0.001	4	5.8	27.6	0.001
		Lake	17	11.1	9.5	0.001	17	7.1	7.2	0.001	17	8.4	9.4	0.001
		Year*Type	17	3.4	2.9	0.03	17	4.8	4.8	0.018	17	3.0	3.3	0.07
		Residuals	318	21.7			160	9.3			230	12.1		
Rotifers	Functional traits	Year	6	4.1	33.2	0.001	3	1.4	64.5	0.001	4	2.8	46.8	0.001
		Lake	17	2.5	7.3	0.001	17	2.3	19.3	0.001	17	2.4	9.3	0.001
		Year*Type	17	1.2	3.4	0.045	17	2.0	16.8	0.001	17	1.0	3.8	0.07
		Residuals	310	6.4			151	1.1			229	3.4		
	Size classes	Year	6	10.2	29.9	0.001	3	3.6	64.2	0.001	4	6.3	48.0	0.001
		Lake	17	9.6	9.9	0.001	17	10.2	31.6	0.001	17	6.3	11.3	0.001
		Year*Type	17	2.5	2.6	0.17	17	5.8	18.0	0.002	17	2.1	3.7	0.10
		Residuals	310	17.6			151	2.9			229	7.6		
Crustacean Zooplankton	Functional traits	Year	6	12.1	43.6	0.001	3	7.6	118.1	0.002	4	9.5	59.4	0.003
		Lake	17	4.7	6.0	0.002	17	3.7	10.2	0.001	17	3.0	4.5	0.002
		Year*Type	17	2.8	3.5	0.002	17	3.9	10.7	0.003	17	2.6	3.8	0.009
		Residuals	316	14.7			157	3.4			229	9.1		
	Size classes	Year	6	12.4	35.0	0.001	3	7.5	86.1	0.004	4	9.2	41.8	0.009
		Lake	17	5.3	5.3	0.001	17	4.0	8.1	0.003	17	3.8	4.1	0.028
		Year*Type	17	3.8	3.8	0.003	17	4.5	9.1	0.005	17	3.6	3.8	0.02
		Residuals	316	18.7			157	4.6			229	12.6		

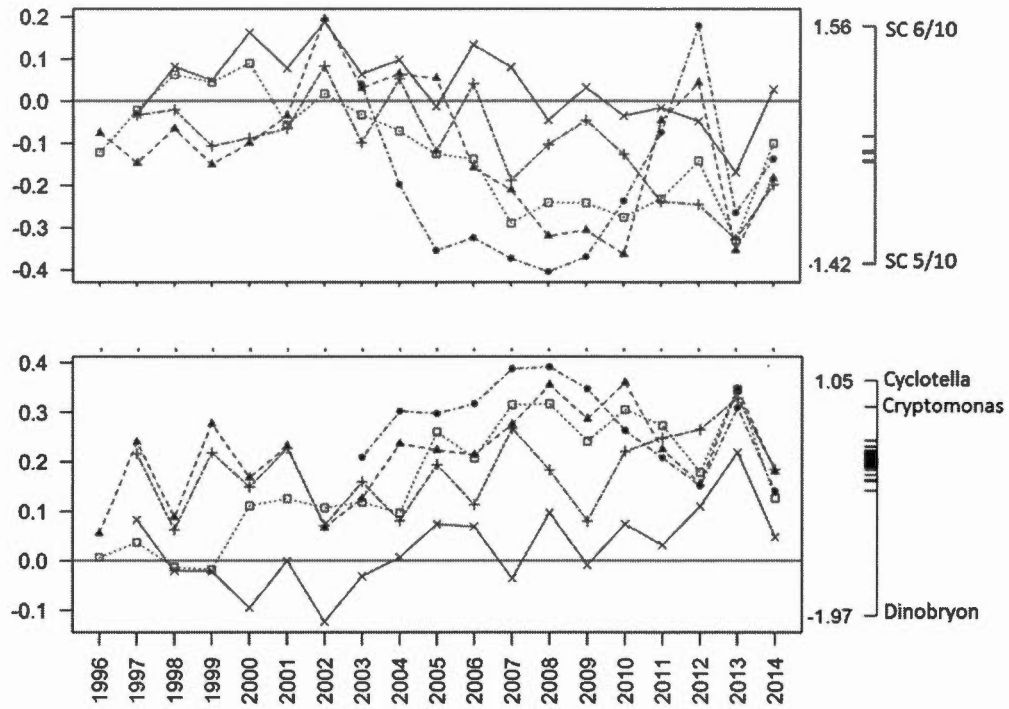

Figure 4.12 Principal response curves for phytoplankton (a) size structure and (b) species composition. Species weights represent which functional traits responded to mining activities. For clarity only traits with an absolute weight > 0.5 are shown.

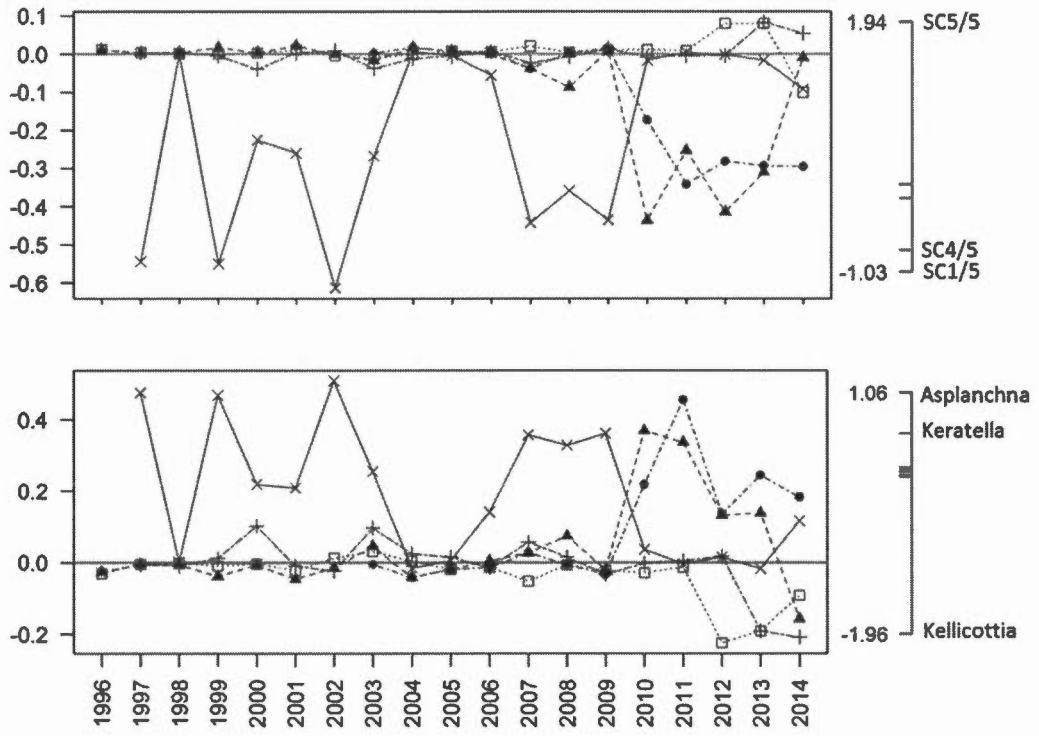

Figure 4.13 Principal response curves for rotifer (a) size structure and (b) species composition. Species weights represent which functional traits responded to mining activities. For clarity only traits with an absolute weight > 0.5 are shown.

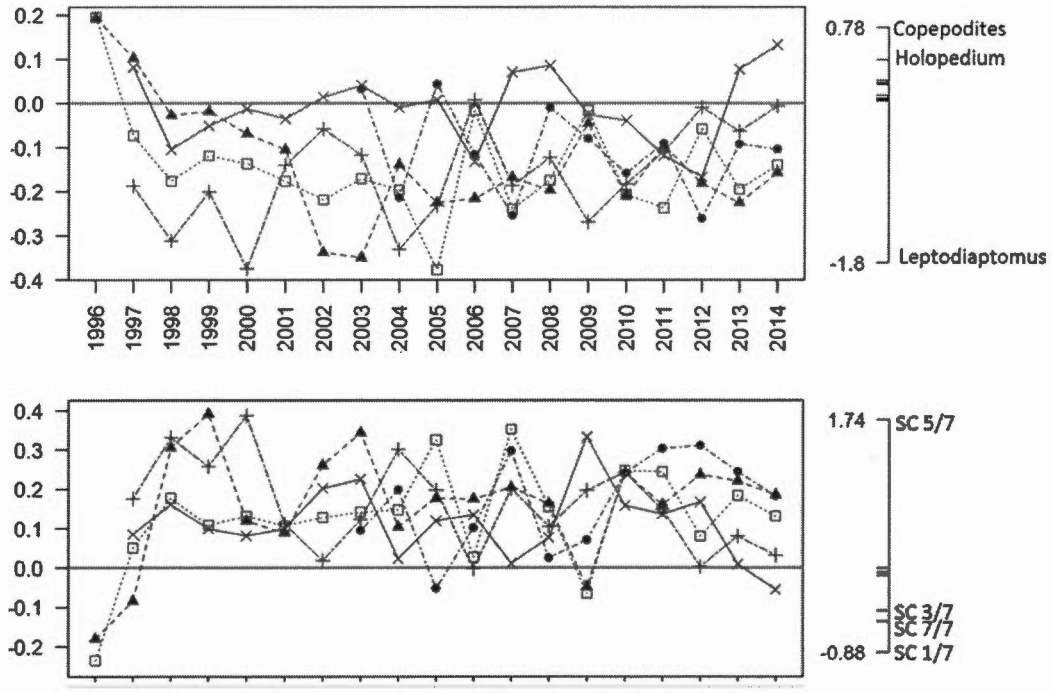

Figure 4.14 Principal response curves for crustacean zooplankton (a) size structure and (b) species composition. Species weights represent which functional traits responded to mining activities. For clarity only traits with an absolute weight > 0.5 are shown.

CONCLUSION

4.8 Objectifs et résultats généraux

Cette thèse, a dressé un portrait des relations complexes entre la structure des communautés planctoniques, leur environnement et leur métabolisme, à l'échelle du paysage des lacs. Pour bien comprendre ces relations, nous avons utilisé une approche séquentielle de laquelle nous avons préalablement examiné les liens existant entre l'environnement et la structure des communautés (Chapitre I) et entre l'environnement et la productivité zooplanctonique (Chapitre II). Par la suite, nous avons utilisé les connaissances acquises dans ces deux chapitres pour comprendre la relation entre la productivité planctonique, la structure fonctionnelle des communautés et l'environnement au niveau du paysage des lacs (Chapitre III). Une des forces de la présente thèse est d'avoir utilisé une approche fonctionnelle qui a permis de mieux comprendre comment les communautés planctoniques affectent et répondent à leur environnement. Nous avons utilisé une approche similaire, mais dans un contexte complètement différent, celui de l'analyse de l'impact d'une mine sur les communautés planctoniques les lacs en aval (Chapitre IV), afin de tester l'applicabilité de nos conclusions dans le contexte d'une perturbation anthropique.

Malgré le fait qu'il existe un fort lien trophique entre le zooplancton et le phytoplancton dans les lacs (Porter, 1977; Carpenter *et al.*, 1985; Sterner, 1989), une des contributions importantes de la présente thèse, est de démontrer qu'au niveau du paysage des lacs (Chapitre I) ce lien trophique ne se traduit pas en un couplage significatif entre la composition taxonomique et fonctionnelle du phytoplancton

et du zooplancton. Cette absence de couplage résulte du fait que la composition des communautés de phytoplancton et du zooplancton dans les lacs tempérés nordiques répondent à différents facteurs environnementaux et spatiaux, et donc que la composition des prédateurs (pour le phytoplancton) et des proies (pour le zooplancton) n'influence pas leurs distributions respectives à grande échelle. Plus précisément, nous avons observé que le phytoplancton répond fortement à son environnement proximal (la qualité de l'eau), tandis que le zooplancton répond plus fortement aux caractéristiques de son habitat (morphométrie du lac).

Cette conclusion a d'importantes implications à plusieurs niveaux. Premièrement, le fait que la distribution du phytoplancton ne soit pas contrainte par la distribution du zooplancton et vice-versa implique qu'un changement important dans la composition d'un des deux groupes au niveau du paysage des lacs n'aura pas nécessairement d'impact sur l'autre niveau trophique. Cette conclusion a été corroborée (Chapitre IV), puisque c'est exactement ce que nous avons constaté en aval de la mine Ekati. En effet, nous avons observé qu'après près d'une vingtaine d'années d'activité minière, et malgré un impact important sur la qualité de l'eau dans les lacs, l'impact sur la composition des communautés planctoniques se limite principalement au phytoplancton. Bien que plus récemment les rotifères ont commencé à répondre, dix ans après une forte réponse au niveau du phytoplancton aucune réponse n'est encore observable pour le zooplancton. La composition taxonomique et fonctionnelle ainsi que la biomasse totale n'ont pas significativement changé. De plus, comme ce fut le cas à l'échelle du paysage des lacs (Chapitre I) nous avons observé dans les lacs en aval de la mine une forte réponse de la composition du phytoplancton aux changements de la qualité de l'eau, le principal effet de l'activité minière. De son côté, le zooplancton, crustacé et rotifère, a répondu d'une façon plus limitée aux changements de la qualité de l'eau, puisque tel que nous l'avons observé (Chapitre I), c'est la morphométrie des lacs qui influence

principalement la composition du zooplancton. La consistance des réponses entre ces deux chapitres démontre comment une approche fonctionnelle est généralisable pour aborder de multiples questions de recherche en écologie aquatique. Tel que supposé par McGill *et al.* (2006) l'utilisation des traits fonctionnels permet en effet de dégager certaines patrons généralisables et ainsi de démontrer que l'écologie des communautés n'est pas un grand désordre (Lawton, 1999; Simberloff, 2004) .

Bien entendu, le découplage observé entre la composition du zooplancton et du phytoplancton autant à l'échelle du paysage des lacs que dans le contexte de lacs miniers, n'implique pas qu'il en sera de même dans toutes les situations. Il fut démontré expérimentalement (Ghadouani et al., 2003) que quand les cyanobactéries dominent, les cladocères sont moins abondants, ce qui est un exemple d'un effet trophique sur la composition. Il serait intéressant de tester si ce patron est aussi observable dans les lacs, ou si comme nous l'avons observé la composition zooplanctonique, répond principalement à leur morphométrie.

Malgré l'absence de couplage, la biomasse de phytoplancton (estimée en utilisant la concentration de chl$a$) est un facteur important influençant la productivité zooplanctonique. Le taux de production de biomasse par le zooplancton crustacé était plus important à l'intérieur des lacs avec une plus grande biomasse de phytoplancton. De plus, nous avons démontré que les principaux facteurs environnementaux influençant l'efficacité des communautés zooplanctoniques à produire de la biomasse au niveau de la communauté sont similaires à ce qu'il avait été précédemment observé au niveau de la population (Downing et Rigler, 1984; Shuter et Ing, 1997; Stockwell et Johannsson, 1997). Nous avons cependant identifié des variables émergentes au niveau de la communauté. Les deux variables émergentes identifiées sont la taille du lac et la proportion de milieux humides au niveau du bassin versant. Suite à ces observations, une de nos suppositions était que ces variables influencent la composition zooplanctonique dans un lac, ce que nous avons

pu confirmer au Chapitre III. Nous avons observé un effet de la taille du lac sur la proportion de *Daphnia*-filtration et un effet de la proportion de milieux humides sur l'équitabilité fonctionnelle. Ces résultats, dans un contexte écosystémique, permettent de mieux comprendre les facteurs qui influencent la productivité des écosystèmes aquatiques et le transfert d'énergie et de matière dans les lacs.

Au Chapitre III, nous avons démontré que les communautés zooplanctoniques, ne peuvent être considérées comme des boites noires et que leur composition a une grande influence sur leur productivité. Nous avons observé que l'importance relative de la structure des communautés pour le zooplancton est comparable à l'importance relative de l'environnement. De plus, nous avons observé que ce n'est pas la diversité qui est importante, mais bien la composition fonctionnelle des organismes dans une communauté. Les communautés planctoniques sont plus productives quand la proportion d'organismes utilisant les stratégies alimentaires de *Daphnia*-filtration et Chydorus-filtration sont dominantes ainsi que lorsque, plus généralement, une stratégie fonctionnelle est fortement dominante à l'intérieur de la communauté. Ces résultats sont en liens directs avec ce qui a été observé dans d'autres études en milieu aquatique (voir Figure 0.1) dans lesquelles la relation observée entre la diversité et la production de biomasse est négative ou non-significative. Plutôt qu'un effet de complémentarité, nous avons observé que c'est l'identité des espèces dominantes qui est importante. Par conséquent, la sélection des types fonctionnels est le principal mécanisme par lequel les communautés planctoniques influencent la productivité zooplanctonique. Dans les lacs, puisque la succession planctonique est très rapide, le type fonctionnel productif change au cours d'une saison, ce qui est capturé par la mesure d'équitabilité fonctionnelle. Cette conclusion a des implications importantes au niveau du paysage des lacs puisque plus que la perte de biodiversité, c'est la perte de certains types fonctionnels dans les lacs qui a le potentiel d'avoir un effet sur un processus

écosystémique tel que la productivité planctonique, du moins, la productivité de zooplancton.

Finalement, nous avons aussi démontré la pertinence d'utiliser une approche fonctionnelle. Cette approche nous a permis d'identifier les traits fonctionnels répondant aux différentes variables environnementales au niveau du paysage des lacs et dans le contexte de lacs miniers. De plus, cette approche a permis d'identifier les traits fonctionnels qui ont un effet sur l'efficacité de la communauté zooplanctonique à produire de la biomasse. Nous croyons donc que, pour mieux comprendre comment les communautés biotiques interagissent avec leur environnement, l'utilisation d'une approche fonctionnelle est grandement pertinente et devrait être favorisée. En utilisant les traits fonctionnels reliés aux interactions trophiques nous avons été en mesure de bien caractériser cet aspect en particulier. À ce niveau, une des limites de notre étude renvoie au nombre limité de traits disponibles. Il serait donc intéressant dans le futur d'être en mesure d'intégrer d'autres traits afin de cerner la réponse fonctionnelle à d'autres niveaux trophiques.

En conclusion, collectivement, les résultats de cette thèse suggèrent qu'a l'échelle du paysage des lacs il existe un lien important entre la structure d'une communauté zooplanctonique et son efficacité à produire de la biomasse, et ce, même après avoir pris en compte l'effet des variations environnementales. Dans le futur, il serait intéressant d'utiliser cette approche afin d'identifier si des patrons similaires sont observés pour d'autres niveaux trophiques aquatiques. De plus, en considérant seulement les interactions trophiques entre le phytoplancton et le zooplancton, nous avons ignoré un pan complet du réseau trophique aquatique ; celui de la matière allochtone qui est mobilisé par le bacterioplancton. Il serait donc intéressant de mieux comprendre l'importance de ce cette autre composante des réseaux trophiques et son influence sur la composition et le métabolisme du zooplancton.

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